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THE BOTANICAL GAZETTE

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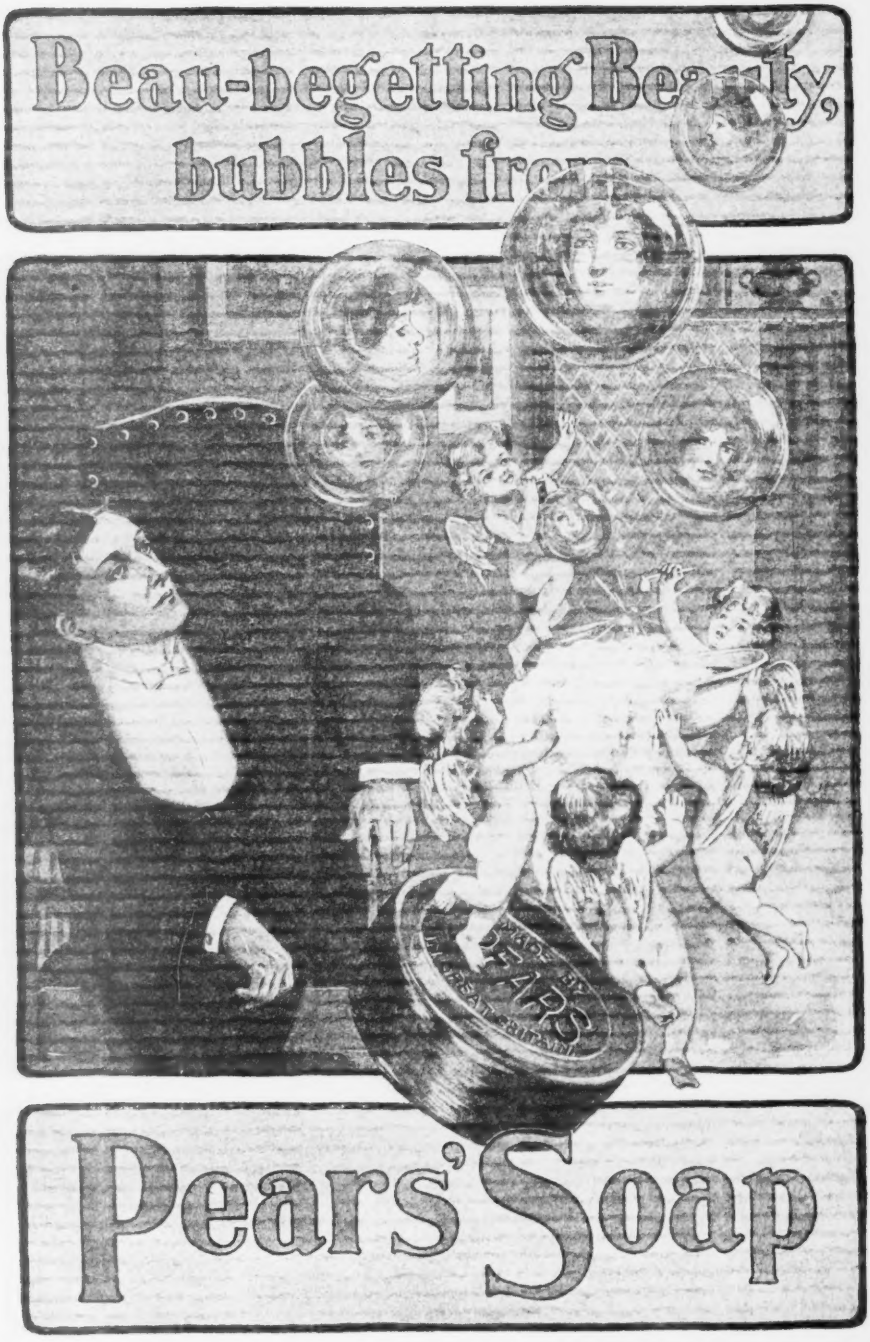

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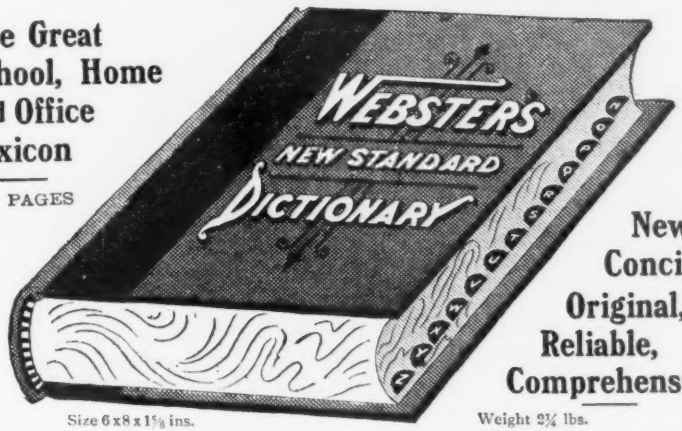

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VOLUME XXXVII NUMBER 1

BOTANICAL GAZETTE

JANUARY, 1904

THE MORPHOLOGY OF ELODEA CANADENSIS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LII.

ROBERT B. WYLIE.

(WITH PLATES I–IV)

THE Helobiales occupy a place of special interest among monocotyledons. Beginning with members having the simplest flowers, the group includes an ascending series of forms and finds its climax in the Hydrocharitaceae which display considerable floral complexity. This series has attracted much attention from plant morphologists and early investigation naturally centered among the simpler members. It was with the hope of adding something to the data concerning one of the higher forms that this study was undertaken Elodea further invites attention on account of its being one of the most specialized of submersed aquatics.

My thanks are due Professor John M. Coulter and Dr. Charles J. Chamberlain for kindly suggestions and valued assistance.

FLORAL DEVELOPMENT.

The flowers of *Elodea canadensis* are usually borne singly in the axils of leaves, and are scattered along the stem in a loose indeterminate inflorescence. They are so far apart, however, being separated by fifteen to twenty internodes, that one flower is well developed before the primordia of the next younger one are established.

The flowers are functionally monosporangiate, though rudiments of the suppressed parts are often present. Three sterile

stamens are commonly found in the pistillate flower, and six have been reported to occur in rarer instances. These staminodia are composed of uniform parenchyma and show no evidence of the suppressed sporangia. Much more unusual is the development of stigmas upon the staminate flower. Eichler (**5**) refers to these as being possibly rudimentary stamens; the writer, however, has found well-developed stigmas above the nine stamens usually borne by the staminate flower. In one instance the stigma was clothed with papillae and covered with pollen grains which had sent their tubes into its tissue. In such a case it would appear that the usual stigmatic secretions are present and that it differs in no essential respect from a normal stigma. Such conditions recall Chamberlain's (**2**) discussion of the teratology of Salix, in which monosporangiate, dioecious genus he reports almost all possible combinations in the production of the sporangia.

The occurrence of these rudiments in Elodea must point back to an ancestry with perfect flowers, and their specialization has no doubt been correlated with the changed conditions of the submersed habitat. The flowers are now dioecious and are peculiarly adapted to the combined influences of wind and water for pollination. The pistillate flower is quite complex and presents one of the most striking cases of epigyny known; the staminate flower is simpler and has acquired the habit of breaking loose from the stem at maturity.

The development of the pistillate flower was studied by Horn (**3**), who also investigated the vegetative plant body; but since his work was based on the external aspects or rough sections only, the account, while accurate in a very general way, lacks most of the details secured through modern methods. The pistillate flower begins as a protuberance from the side of the stem near the growing point (*fig. 1*). This swelling pushes out rapidly, soon equaling the stem tip in length and giving it the appearance of having bifurcated (*fig. 2*), but the main axis soon reasserts its dominance, leaving the flower as a distinctly lateral member (*fig. 3*). At this time ridges near the base of the flower mark the origin of the spathe (*fig. 2*), which pushes out rapidly and for a long time envelops the developing flower (*figs. 2–12*).

The apex of the receptacle now flattens and broadens slightly, and, with the earliest indication of the floral parts, a cylindrical mass of tissue grows up (*figs. 5–10*), leaving a triradiate slit down its center, the walls being closely pressed together. The various parts of the flower continue meanwhile to develop at the outer end of this rapidly elongating growth. The calyx pushes out first (*fig. 5*), the sepals soon curving over the growing parts within; next comes the whorl of three sterile stamens (*figs. 8–9*), followed by the three stigmas (*figs. 10–12*); last of all appears the corolla (*figs. 11–12*).

Simultaneous with the development of the stigmas at the outer end of this floral tube is the growth of the ovules within its base. These push out from the surfaces of the central opening (*fig. 10*), but it is only as they develop that traces of the ovarian cavity appear (*fig. 11*). The walls which have previously remained in contact are now pushed apart, forming the rounded triangular ovary (*fig. 12*). The parts above ultimately coalesce, roofing over the cavity.

The various parts of the flower having been established, the floral tube, that region of fused parts between ovary and sepals, enters upon a period of more rapid elongation. The direction of growth is at first a negative geotropic response, and the young flowers stand up quite stiffly, but during later development proper orientation is probably due entirely to the buoyancy of the enclosed gases. Very early in the history of the flower the beginnings of three rows of air spaces can be seen, extending through its whole length (*fig. 11*). These start as rifts between cells and increase in size with the growth of the flower (*fig. 12*), until at maturity they constitute a large part of its volume. It is the low specific gravity of the floral tube that insures its direction toward the surface of the water, as these parts are very weak and cannot support themselves. A cross-section of the floral tube shows an outer ring, composed of two layers of cells, and a central conducting strand joined to the outer part by three bridges of tissue, leaving the three rows of air spaces between. The outer wall has no stored food, but all other cells are richly provided with starch.

The adult pistillate flower presents unusual proportions; the diameter of the floral tube is about 0.3 mm, while its length in extreme cases may be over 30 cm, in such an instance the flower being one thousand times longer than wide. The lower part is invested by the spathe, which is 2 to 3 cm long. The sessile ovary at the time of pollination is about 4 mm long and less than 1 mm in diameter.

The staminate flower originates in the same general manner as the pistillate, and in early stages they might easily be confused. The later development of the pollen-bearing flower differs markedly, as it shows none of the complexities described above. The receptacle, instead of pushing up into a floral tube, becomes merely conical, and gives rise in turn to sepals, outer stamens, inner stamens, and very much later the corolla, which is not prominent and may be quite rudimentary (*figs. 13–22*). A conical protuberance is often seen in the center of the flower to which the inner stamens may be adnate for a part of their length (*fig. 22*). That part of the pedicel between the insertions of spathe and sepals elongates slightly and develops large air chambers (*fig. 22*). It is at the upper end of this region that the break occurs which sets free the flower at maturity. The exact mode of detachment was not determined.

THE FEMALE GAMETOPHYTE.

The female gametophyte is developed while the floral tube is elongating toward the surface of the water. The tube had a length of about 4 mm when the primary sporogenous cell was established; was twice that long when the ovule contained a 2-celled embryo sac; and had attained a length of 15 mm at the 8-celled stage.

The single archesporial cell (*fig. 23*) cuts off a primary parietal cell which ordinarily divides first by an anticlinal wall (*fig. 24*). The details of development of the parietal tissue were not studied, but it seems to be very limited in amount and probably does not persist long.

The primary sporogenous cell enlarges greatly, and in its division the spindle lies wholly in the outer half of the cell (*fig. 25*). The resultant cells differ greatly in size, the deeper one

being six or eight times larger than the micropylar one. In the division of these daughter-cells the spindles show a corresponding difference in size and vary in direction, especially in the outer cell, in which it may lie at right angles to the longer axis of the ovule (*figs. 26, 27*). Four megaspores are usually formed, which are separated by walls. In one instance it was observed that the two central cells of the row of four had each divided again, resulting in six megaspores (*fig. 28*). This case was made very clear as the megaspore at either end of the row had enlarged, thus lessening the possibility of confusing sterile cells with megaspores. This particular row is of interest also in showing a struggle for dominance between the innermost and outermost cells. In all other cases noted there were but four megaspores, and the innermost one seems regularly to be the successful one (*fig. 29*).

With the division of the megaspore there is introduced a change in the form of the embryo sac, which, though often seen in later development, is seldom introduced at so early a stage. The upper one-third of the embryo sac begins to enlarge, and by the time this first division is completed has a diameter nearly twice that of the cylindrical part beneath (*fig. 30*). As development proceeds this differentiation becomes more marked. The outer part, in which all the growth takes place, continues to enlarge, being at first spherical, then oblong, and finally assuming the usual embryo sac form. The inner part persists with dimensions unchanged or somewhat diminished by encroachments of the main body of the embryo sac (*figs. 31–36*). While such a pouch-like antipodal end is not uncommon, the emphasis laid on its early development in this instance might suggest its being a rudiment of a once prominent nutritive device, but it probably functions now in no important way.

At the two-celled stage one nucleus passes to each end of the sac (*fig. 30*). The divisions giving rise to the antipodal group occur deep within the pouch (*figs. 31, 32*). The spindles seen here are much smaller than those of the micropylar end, and the resultant nuclei of the two groups show a proportional difference in size (*fig. 32*).

The antipodal polar appears regularly to issue from the pouch at an early stage, and as it passes into the body of the embryo sac it increases in size, until at the time it arrives in the vicinity of the other polar no difference in their dimensions is discernible (*figs. 34, 41, 42*). The polars soon approach one another and may remain for a long time in contact. Their actual fusion was not observed and seems not to occur until the time of fertilization. Shibata (**14**) has shown for Monotropa that pollination hastens the fusion of the polars. In Elodea neither pollination nor the entrance of pollen tubes into the ovary constitutes a sufficient stimulus. In ovules which have failed to receive pollen tubes the polars may still be seen lying side by side, even though surrounded in the same ovarian cavity by other ovules whose eggs have been fertilized, and which contain embryos. The actual presence of the pollen tube in the ovule seems to be necessary to bring about their union. Guignard (**9**) has shown a similar behavior of polars in Capsella. In this form the polar nuclei are distinct until the male elements penetrate into the embryo sac; their union appears to be accomplished, however, before fertilization takes place.

The antipodals always remain in the pouch in which they were formed, and before the entrance of the pollen tube are inconspicuous and stain feebly. At the time of fertilization, however, and during the early development of the embryo, some activity is manifest in this region. The group then generally shows a fourth nucleus (*figs. 35, 36, 38, 39*), the uppermost of which becomes quite large and may have more than one nucleolus. This enlarged nucleus is often surrounded by a considerable mass of cytoplasm which may be enclosed by a definite membrane, giving it the appearance of an egg (*figs. 38, 40*). In rarer instances two enlarged nuclei are seen, making five in all (*fig. 37*), while not uncommonly the tip displays the usual number, three (*fig. 40*).

The sudden appearance of the extra nucleus in the antipodal group, when one has in mind the behavior of the polars, might suggest that these nuclei do not always fuse, and that one of them passes down to the lower end of the embryo sac and joins

those in the antipodal pouch. The general evidence, however, is against this view. The irregular number of nuclei displayed here and the general arrangement of the cytoplasm about them would indicate that any increase in number has come from divisions among the antipodals—an activity in this region that often results from fertilization. In all embryo sacs studied at earlier stages the lower polar had passed out of the tip, and its return to the antipodal group seems here improbable.

THE MICROSPORANGIUM.

The stamens are very short-stalked, the sporangia being practically sessile, and are further characterized by a relatively small amount of sterile tissue. Each stamen develops only two sporangia, there being no suggestion of a greater number at any stage. This condition seems to occur regularly in but a limited number of forms. The presence of only two sporangia to the stamen has long been known for the Asclepiadaceae, and has recently been reported by Shoemaker (**15**) for Hamamelis. The occurrence of this phenomenon in such widely separated and differently specialized forms offers no clue to its significance.

The developing stamen is at first circular, later becoming oblong in cross-section. From a homogeneous meristematic mass there differentiates at either side of the stamen a hypodermal archesporial column (*fig. 43*). These cylinders of tissue extend the whole length of the stamen and have from five to eight cells each in cross-section. They are separated by a mass of sterile cells which later develops the rudimentary bundle and contributes somewhat to the tapetum of both sporangia. The archesporial cells become quite distinct, differing from these sterile cells in size and staining reactions.

In the establishment of the primary wall layer the divisions of the archesporial cells are not simultaneous, the outer ones tending to divide a little earlier than those nearer the body of the stamen. It follows, from the form of the stamen and the extent and location of the archesporium, that the primary wall layer nearly invests the column of primary sporogenous cells, and this investment is made more nearly complete in places by the

introduction of curved walls at the axial corners of the archesporium (*fig. 44*). While in no observed instance was the inclosure quite complete at this time, it was noted that a little later the cells on the axial side may divide (*fig. 45*), thus bridging the gap in the wall layer. Coulter (**3**) has shown that in Ranunculus a part of the tapetum may come from the sporogenous tissue. Rosenberg (**12**) finds in Zostera that the tapetum on both the inner and outer sides can be traced back to the divisions of the greatly elongated sporogenous cells. In Elodea these divisions of sporogenous cells on the axial side seem to be of common occurrence, and there is probably a regular contribution to the tapetum from the sporogenous cells in that region. In addition there may be a contribution to the diffuse tapetum on any side by the sacrificing of potential spore mother-cells to the nutritive function. When the time of spore formation is at hand the functioning mother-cells are fewer than were the primary sporogenous cells, notwithstanding divisions may often take place among these tending to increase their number. The successful spore mother-cells become greatly enlarged before their division (*fig. 47*). A cross-section of the sporangium at this time may show only one of these cells, the others having broken down, though commonly there are three side by side (*fig. 46*), and portions of four are often seen in a given section.

The primary wall cells form a zone several layers of cells in thickness, of which the outer one only, the endothecium, persists until the discharge of the spores.

THE MALE GAMETOPHYTE.

The male gametophyte is considered to have begun with the spore mother-cells. Both the first and second divisions of the mother-cells are characterized by slender curved spindles terminating at either end in the plasmatic membrane (*figs. 48, 49*). Such spindles have been figured by Strasburger (**16**) for Ceratophyllum. Following the first division a delicate wall is formed, dividing the mass into two hemispherical cells. The nuclei of these daughter-cells are greatly elongated. The number of chromosomes was not made out with certainty, but is probably twelve for the gametophyte.

In the second division the spindles commonly lie parallel, in which case the four spores of the tetrad develop in one plane; but the spindles may be rotated so that their planes intersect at right angles, resulting in a correspondingly different grouping of the pollen grains. Following the second division, the four microspores are organized in the usual manner. The young spores lie for a time within the wall of the mother-cell (*fig. 50*), but the small tetrads soon appear naked (*fig. 51*) and enter upon a period of rapid enlargement. The four members of the tetrad do not fall apart, but remain attached and are ultimately shed from the sporangium still firmly joined together. This union is so intimate at maturity that violent shaking in a closed vessel partly filled with water seldom breaks them apart.

Though borne by one of the most specialized of submersed aquatics, a plant entirely devoid of cutinized walls in all its vegetative parts, the microspores of Elodea exhibit a strongly cutinized exine and a well-developed intine. In this connection it is interesting to note that in Naias and Zannichellia, also submersed aquatics, Campbell (**1**) finds no exine developed. Strasburger (**16**) reports for Ceratophyllum, which has a similar habitat, a pollen grain without intine and with a thin smooth exine which is cutinized, but not nearly so strongly as in air blooming plants. In Elodea the exine closely resembles such coats borne in normal aerial sporangia, and is beset with multitudes of spines, which play an important part in the process of pollination, as we shall see later. These spines (*fig. 67*) are cylindrical, with conical points barbed at the base and each bearing at its tip a tiny disk.

The intine possesses in numerous instances peculiar thickenings reaching into the cavity of the spore. These ingrowths may be merely papillae, though they are often rod-like, or even membranous, forming trabeculae extending well across the pollen grain. These protrusions are integrated with the intine at their junctions, and appear to be perfectly uniform in character and substance with it.

The microspore nucleus divides long before the pollen grain has attained its full size (*fig. 52*), and at a time when the spore wall is not yet differentiated into two layers. This first division

appears to be simultaneous in the four spores of a given tetrad (*fig. 53*), though widely varying stages may be found within a single sporangium. The spindle fibers in this division after the cell plate is laid down are much more prominent on the tube nucleus side (*fig. 54*). The generative cell when first cut off along the wall of the spore is crescentic in outline, with a greatly elongated nucleus, but it soon becomes lenticular in form. Later, after its passage into the cytoplasm of the tube cell, it is for a time spherical (*fig. 55*); subsequently it becomes greatly elongated, and just before its division into the male cells is curved and may extend nearly across the spore (*fig. 57*).

The tube nucleus enlarges soon after its formation so as to become very conspicuous. It is at first spherical (*fig. 54*), but a little later becomes amoeboid in shape and assumes the most varied forms, accompanied by a changed reaction to stains (*fig. 56*). Shortly before the division of the generative cell the tube nucleus regains its original form; with the organization of the male cells, however, it may again exhibit irregularities of outline. Schaffner (**13**) in his studies of Erythronium found the generative cell very large and displaying such general activities as are here associated with the tube nucleus.

The formation of the male cells seems to occur regularly long before the pollen grains are shed from the sporangium. The spindle formed within the long crescentic generative cell is itself slightly curved (*fig. 58*), and the daughter nuclei retreat quite far apart before the partition is formed between them (*figs. 61, 62*). The male cells when first organized remain for some time end to end in the relation occupied at the time of their formation, and thus continue the bow-shaped outline which characterized the generative cell. Subsequently, with the symmetrical elongation of both male cells, their adjoined ends become long drawn out, yet still remain attached by their tips. This point of union acts like a hinge, permitting the cells to take the most varied positions with respect to one another, even swinging about so as to lie side by side (*figs. 63–66*). In no observed instance did the male nuclei lie far enough apart to preclude the possibility of their cells being still united by these elongated

ends. As will be seen later, there is reason for believing the male cells of Elodea make the greater part of the journey through the pollen tube still hitched together in this tandem fashion.

During their continuance in the pollen grain the male structures clearly reveal their morphology as cells. About the nucleus, which usually shows a nucleolus, there is an extensive mass of cytoplasm differing considerably from the contents of the spore, and all clearly invested by a limiting membrane. It was observed that one or two more deeply staining bodies usually lie outside the nucleus along the median line of the cell (*figs. 64, 65*); if two of these are present, one lies at each side of the nucleus, though at varying distances from it.

PHENOMENA OF POLLINATION.

While the general mode of pollination in Elodea is well known, the details, which seem never to have been published, are of such interest as to merit a brief description.

The staminate flowers are borne entirely beneath the surface of the water, and these, as is well known, break off and rise to the surface, there shedding the pollen. It is probable that with the ripening of the sporangia, in the still submerged flower, gases given off by the plant fill the spaces about the spores as well as any other cavities developed in the flower. At maturity a bubble of oxygen forms at the tip of the flower, and with its enlargement the sepals open slightly. At this time, looking down into the flower one can see that the sporangia have opened, and that many of the spores have been shed into the central space. The oxygen bubble may finally become nearly as large as the flower, and, when conditions are proper, the buoyancy of the enclosed gas, aided by the low specific gravity of the flower itself, overcomes the weakened attachment, and the flower darts to the surface. Upon reaching the surface the bubble disappears, the sepals snap back quickly, and in their recurved position form three boat-like floats which support the sporangia above the water; these catch the breeze and the flower sails away. While such float devices for the staminate flower are thought to be of great importance in the pollination of Vallisneria, it is doubtful

if any significance can be attached to them in Elodea. The pollen was nearly all discharged at the moment the flower came to the surface, and any remaining portion would have no better opportunity for reaching the stigma of the pistillate flower. The snow-white tetrads are quite conspicuous floating on the water, or scudding along the surface with the wind.

The floating of the pollen grains is due to the nature of the outer spore coat. In a previous paragraph it was mentioned that the exine was covered with spines, each bearing at its tip a slight enlargement; these spines tend to hold back the surface film from contact with the body of the spore, and thus imprison enough air to keep it afloat. The microspore has a greater specific gravity than water, and will sink at once if wetted. This can be demonstrated easily by placing the spores in dilute alcohol, then transferring quickly to water. A simpler and more striking method is to float a quantity of these spores on the surface of water half filling a stender dish; then cover and shake vigorously for a moment. The violent agitation of the water breaks the surface film, permitting the liquid to come into more intimate contact with the body of the spores, which sink at once to the bottom of the vessel.

While the gas bubbles may not be necessary for pollination, they are certainly very helpful. Their buoyancy aids in detaching the flowers, raises them quickly to the surface, and the sudden recurving of the sepals may be related in some way to the escape of the bubbles on reaching the air. The accumulation of gas about the spores in the submerged flower is also of significance in that it prevents the moistening of the ripe spores while yet submerged; for this, as we have seen, would lead to their sinking upon release. The general relation of these accumulations of oxygen is shown by the fact that in quiet waters of aquaria the rapid appearance of the staminate flowers at the surface of the water is simultaneous with the first marked photosynthesis of the day. During the early part of the forenoon the flowers which have ripened during the hours of darkness are rapidly brought up as the liberation of gas by the plant is increased, and very few appear in afternoon or evening.

The pistillate flower, as has been noted above, reaches the surface of the water by the lengthening of the fused parts above the ovary. Elongation does not cease immediately upon reaching the surface, as there is usually developed some surplus length before the floral parts open. These parts are repellent to water and so resist wetting for many hours. With the opening of the flower the three prominent stigmas quickly recurve, arching well out over the floral envelopes. Lying thus, commonly on its side at first, the weight of the flowers rests chiefly upon the stigmas. Since the stigmas are not readily wetted by water, they form a depression in the surface film. Pollen grains floating near the flower therefore approach and quickly slide down into contact with the stigma. There is thus established about each flower "a circle of influence," which in quiet waters is about 2 cm in diameter, and spores floating into this area are immediately brought into contact with the stigma. When numerous, pollen grains may form a layer lining the bottom of the depression. If at such a time the flower is submerged, as may happen from wave action, etc., the surface film binds together floral parts and spores as they pass beneath the water, and invests them with a considerable volume of air. When all again come to the surface the pollen grains may be seen sprinkled over all parts of the flower including the other stigmas. Spores lodged against any part of the flower may in this way be transferred to the stigmas.

It will be seen that the whole process of pollination is dependent in one way or another upon the *surface film* of water: (1) such a film makes possible the accumulation of oxygen bubbles within and above the staminate flowers, with whatever of advantage that may follow; (2) it is directly responsible for the floating of the pollen grains on the surface of the water; (3) the surface film brings the floating pollen grains into contact with the stigmas of the pistillate flower.

THE POLLEN TUBE.

As might be expected, considering the remarkable morphology of the pistillate flower, the study of the pollen tube was not without interest. These growths not only have great length, 5–30 cm, but are quite large and display some unusual activities.

While the formation of the pollen tube was not studied in detail, it seems to take place in the usual way. Microspores germinating on the stigma show the male cells still distinct (*fig. 69*). In no observed instance did all the spores of a group develop tubes; usually only one or two members of the tetrad germinate, the others being held back from the stigmatic secretions. The tubes show very prominently in cross-sections of the flower. They pass down the central conducting strand; occasionally one may be seen in one of the air chambers, but serial sections generally show it to be only a loop put out from the central tissue.

Having reached the upper end of the ovary, the pollen tubes pass with singular directness down through the ovarian cavity to the upturned micropyles of the ovules. One can but remark the efficiency of the chemotropism and the precision with which the tubes pass to the openings in the ovules (*fig. 75*). Few to many curved, tangled, and feebly staining pollen tubes are usually present among the fertilized ovules in the cavity. These seem to have come into the ovary too late; at any rate, the functioning pollen tubes are always much straighter and stain more deeply than the ones which have failed to enter the ovules.

It not infrequently happens that one of these functionless pollen tubes, having failed to enter a micropyle, may swell up at its tip and terminate its development in a cyst-like enlargement (*figs. 70–74*). Scores of these growths were encountered in material of all stages of development after fertilization, collected through two seasons from various stations, and killed in different ways. Their occurrence, therefore, is so uniform as to merit some attention, especially as they do not seem to have been discussed in connection with any other plant. These cystoids may be found lying anywhere in the cavity of the ovary, but seem never to occur in the style nor in any tissue through which the tube passes. They may lie along the walls of the cavity or in contact with the ovules, but usually are free in cavity of the ovary. In form they vary from spherical to oblong; some may be irregular in outline or even lobed, while those in contact with the wall or ovule are often much flattened or elongated (*fig. 74*).

These enlargements vary in size from slight swellings to growths ten or fifteen times the normal diameter of the tube. Their contents were studied with interest, as it seemed they might throw light on the nuclear conditions in the pollen tube. Their staining properties are uniform with those of the ordinary pollen tube, and nuclei are nearly always present, sometimes evidently disorganizing (*fig. 73*), but in other cases presenting a normal appearance. The tube nucleus was often quite conspicuous, but it was of special interest to note that in certain of these cystoids the male cells could be distinctly made out (*figs. 70, 71, 72, 74*). Each presented, under favorable conditions, its characteristic appearance. The ample cytoplasm was bounded by a definite membrane and showed within a distinct nucleus with its nucleolus. It was also noted that these male cells generally lie near one another, as though still joined together, and in certain cases this connection was very evident (*figs. 70, 74*).

The presence of the male structures as distinct cells in these cystoids lying among the ovules affords very definite information as to their condition during the journey through the pollen tube, and it is obvious that they have retained the features that characterized them in the pollen grain. Guignard (**6**) has contended that the male structures are found as cells in the pollen tubes of Lilium, though this is denied by Koernicke (**4**). More recently Guignard (**9**) has reported a similar condition for Lepidium, which unfortunately is accompanied by no satisfactory figure. Since the tubes producing these cystoids in Elodea may be longer than the functioning ones, and apparently differ from them in no essential respect, it is probable that, in this form at least, the male structures regularly maintain their integrity as cells until they come into the vicinity of the micropyle.

The pollen tubes of Elodea, furthermore, are remarkable for their persistence. Long after fertilization the enlarged tip of the pollen tube may be seen clearly outlined by the side of the suspensor cell (*figs. 78–83*), while stretching upward from the micropyle into the cavity of the ovary extends the tube still darkly staining and apparently turgid. These conditions persist until the embryo is well developed. Those portions of the tube

in the ovary more removed from the ovules show diminished contents or may be empty, but their course can be readily followed in the floral tube where the protoplasm is massed into the deeply staining "Propfen." The cystoids likewise remain long among the enlarging ovules, but their adjoined tubes, which are never conspicuous, soon collapse. All other functionless tubes seem quickly to perish in the ovary.

The male gametophyte as represented by the pollen tube, therefore, both in size and in length of life becomes a conspicuous generation. It is at first nourished by the stored foods of the spore and conducting tissue. After fertilization, with the growth of the ovary, connection is severed between the part in the floral tube and that near the micropyle, the lower end continuing to live apparently parasitically on the embryo sac for a time.

FERTILIZATION.

The pollen tube is usually much contorted in its passage through the micropyle, and upon reaching the embryo sac it swells out in bulbous fashion, at the same time causing one of the synergids to disappear. The whole region is so disturbed by the vigor of the tube that the fate of this cell could not be certainly determined, but appearances indicate that the pollen tube may have passed into the synergid inflating it (*figs. 76–82*). It often happens that two pollen tubes pass into one ovule; in such cases both synergids disappear, and a favorable view of the embryo sac shows the two swollen, darkly staining tips of the pollen tubes arranged symmetrically side by side (*fig. 75*), as though growth of each had been stopped at a certain point. In one instance where three tubes had passed in through one micropyle the whole upper half of the embryo sac was filled by their contents. Guignard (**8**) has reported that in *Nicotiana Tabacum* and *Datura laevis* the pollen tube passes into one of the synergids.

The male cells were not seen in the embryo sac before fertilization. Numerous preparations showed one male nucleus in contact with the egg, and the fate of the second male nucleus was determined in a few cases when it was found uniting with

the endosperm nucleus (*figs. 35, 36*). In all instances but one the male nuclei seen in the embryo sac were in resting condition.

THE EMBRYO.

The oospore divides by a transverse wall. The upper nucleus retreats toward the micropyle and becomes the center of the vesicular cell, which later becomes enormously enlarged. The endosperm nucleus does not divide until a two-celled embryo is established. In many cases the oospore was found dividing with the endosperm nucleus still in resting condition (*fig. 76*); in other instances the endosperm nucleus was in mitosis, but the egg fully divided (*fig. 77*). Figures were never seen in both at the same time. Such a tardy division of the endosperm nucleus seems very rare. Guignard (**7**) has figured for *Naias major* the primary endosperm nucleus in the spirem stage by the side of a two-celled embryo. Hall (**10**) also finds in *Limnocharis emarginata* two nuclei in the young embryo before "the upper polar, which forms the endosperm, has gone through the first division."

A proembryo of four or five cells is established before the end cell divides by a vertical wall (*fig. 79*). While the development of the embryo was not studied in detail, certain variations were noted in these earlier divisions. The basal cell becomes very prominent. When the parts of the embryo are established, this cell has a volume fully forty times that shown in *fig. 82*, and when the seed is nearly ripe it still shows prominently, though somewhat flattened, at the root end of the embryo (*fig. 83*). The remaining synergid also often enlarges for a time nearly as rapidly as the suspensor cell (*fig. 81*), and seems during the early stages to share with it a common function.

The embryo seems to be of the usual monocotyledonous type. The primary root probably does not function, and secondary roots are seen in the seed pushing out near the base of the stem (*fig. 83*).

SUMMARY.

1. The pistillate flower is strongly epigynous, and develops a long floral tube reaching from the sessile ovary to the surface of the water.

2. Four megaspores are usually formed; six were noted in one instance.

3. The embryo sac early develops a pouch in which the antipodal group of nuclei is formed.

4. The polars approach one another at an early stage and may remain for a long time side by side; their fusion, however, was not noted before fertilization.

5. The stamens regularly produce two sporangia each. The primary wall layer nearly invests the sporogenous tissue, which later may contribute to the tapetum on the axial side.

6. The pollen grains adhere in tetrads and have a greater specific gravity than water. The exine possesses spines which hold back the surface film and imprison sufficient air to keep the spores afloat.

7. The male cells are organized in the pollen grain and are joined together by their elongated ends.

8. Gas bubbles aid in detaching the staminate flowers and in bringing them promptly to the surface of the water.

9. The pistillate flower is impervious to water and so produces a depression in the surface film. Pollen grains floating near are brought into contact with the stigmas by means of gravity operating through the declined surface film.

10. The large pollen tubes, having penetrated the long floral tube, pass directly through the ovarian cavity to the upturned micropyles of the ovules.

11. Pollen tubes which have failed to enter ovules often swell up into cyst-like enlargements in the ovary. In these cystoids the male structures can be seen as distinct cells instead of nuclei only.

12. Fertilization takes place in the usual manner, and the second male cell was found uniting with the endosperm nucleus.

13. The primary endosperm nucleus does not divide until a two-celled embryo is established.

14. The pollen tubes persist until the embryos are well developed.

15. The suspensor cell of the embryo becomes enormously enlarged and the synergid often increases in size. The primary

root probably does not function, and secondary roots are developed in the seed from the lower parts of the stem.

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EXPLANATION OF PLATES I–IV.

All figures were made with Bausch and Lomb camera lucida, and original drawings were reduced one-half in reproduction. Figures with magnification greater than 600 diameters were made with Zeiss apochromatic objective 2^{mm}, 1.30 N. A., and Zeiss compensating oculars 4 and 12. All others with Spencer 5^{mm} and 16^{mm} objectives and oculars 4 and 8. The original

magnifications in diameters were approximately as follows: figs. 1–22, 120; 23–42, 850; 43–66, 670; 67, 2300; 68, 69, 670; 70–74, 850; 75, 380; 76, 77, 850; 78–82, 600; 83, 30.

The abbreviations employed in describing figures are as follows: *a*, air cavity; *ar*, archesporium, *at*, antipodals; *e*, egg; *en*, endosperm nucleus; *fl*, flower; *g*, generative cell; *m*, male cell; *o*, ovule; *p*, petal; *po*, polar; *pt*, pollen tube; *s*, sepal; *sg*, synergid; *smc*, spore mother-cells; *sp*, sperm; *spt*, spathe; *st*, stem; *stg*, stigma; *stm*, stamen; *t*, tube nucleus; *v*, vesicular cell; *w*, primary wall cell.

PLATE I.

FIG. 1. Early stage in the development of pistillate flower. Flower seen at side of stem.

FIG. 2. Flower grown out, nearly equaling stem tip in length. Spathe pushing out at base of flower.

FIG. 3. Stem tip resuming original direction. Receptacle flattens.

FIGS. 4–6. Stages immediately preceding development of the floral tube. Calyx showing at margin of receptacle.

FIGS. 7–9. Early development of floral tube. Sterile stamens next to calyx.

FIG. 10. Stigmas and ovules developing simultaneously.

FIG. 11. Later stage showing beginning of corolla.

FIG. 12. Pistillate flower with principal parts all established, and floral tube entering upon period of more rapid elongation.

FIGS. 13–16. Early stages of staminate flower.

FIG. 17. Outer stamens showing next to calyx.

FIGS. 18–20. Development of stamens.

FIG. 21. Corolla growing up between calyx and outer stamens.

FIG. 22. Later stage in development of staminate flower.

PLATE II.

FIG. 23. Early stage in development of ovule, showing archesporial cell.

FIG. 24. Primary sporogenous cell and two parietal cells.

FIG. 25. Division of primary sporogenous cell.

FIGS. 26, 27. Division of daughter cells.

FIG. 28. Ovule with six megaspores. The two central cells of the row of four have each divided, making six in all. The innermost and outermost megaspores developing.

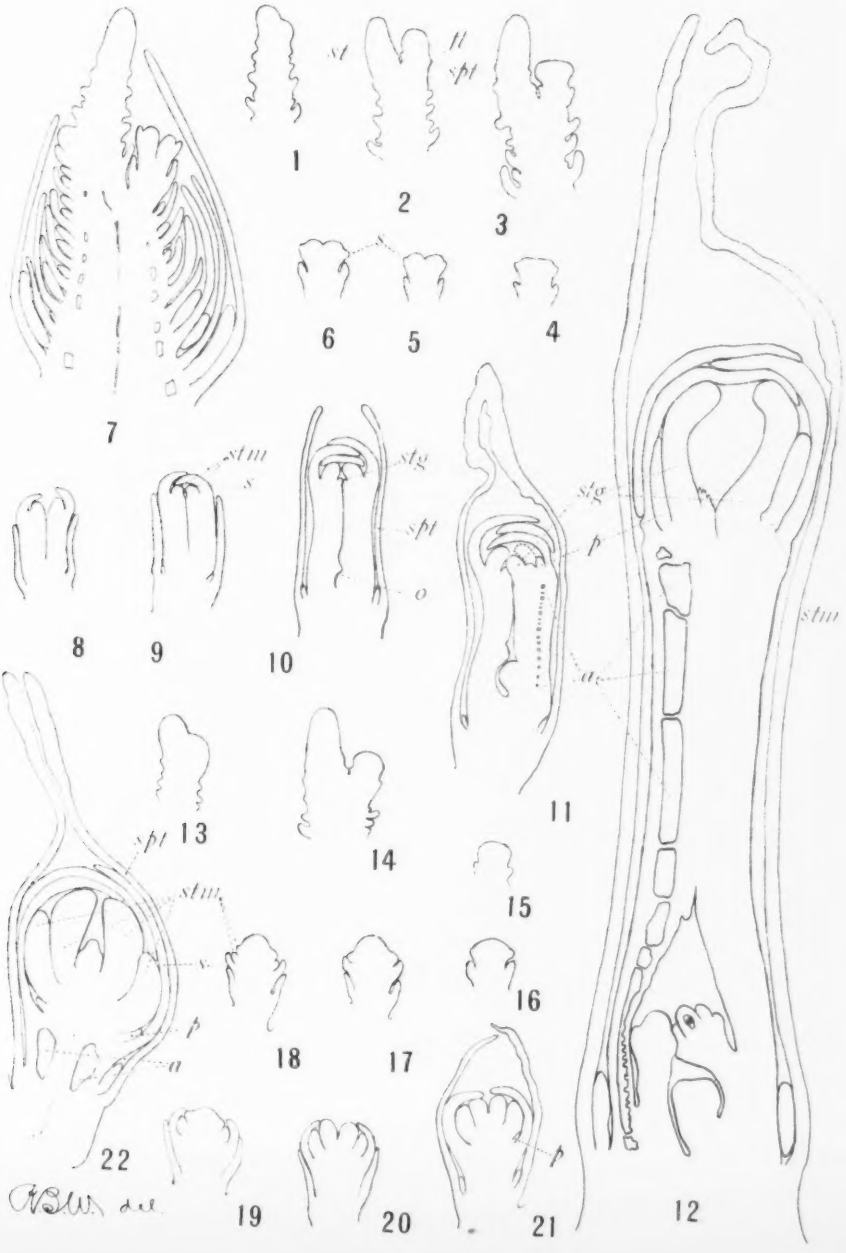
FIG. 29. Row of four megaspores. The deeper-lying one is developing and others are being crowded out.

FIG. 30. Two-celled embryo sac, showing early development of antipodal pouch.

FIG. 31. Division of these nuclei.

FIG. 32. Establishment of 8-celled embryo sac.

FIG. 33. Older embryo sac showing arrangement of cells. Polars approaching one another.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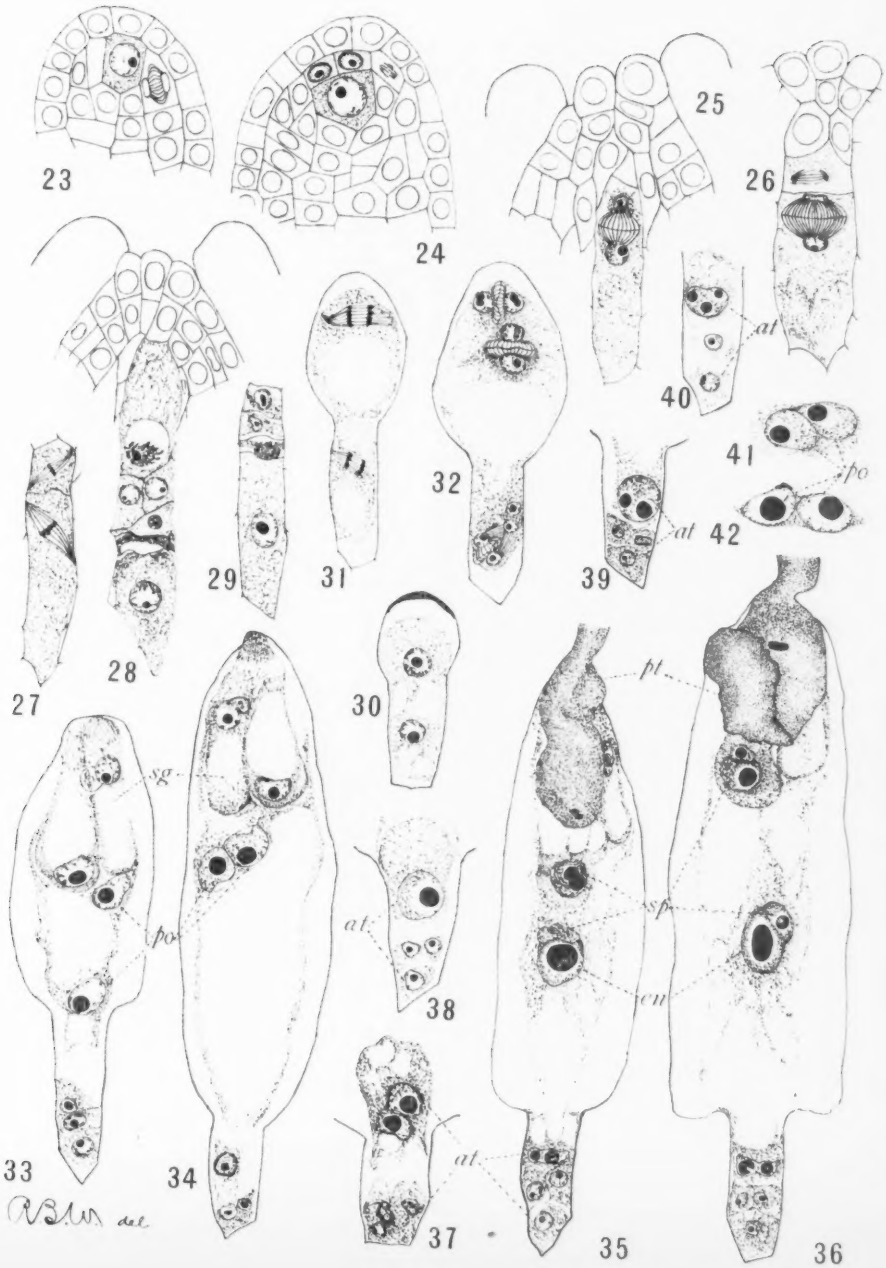
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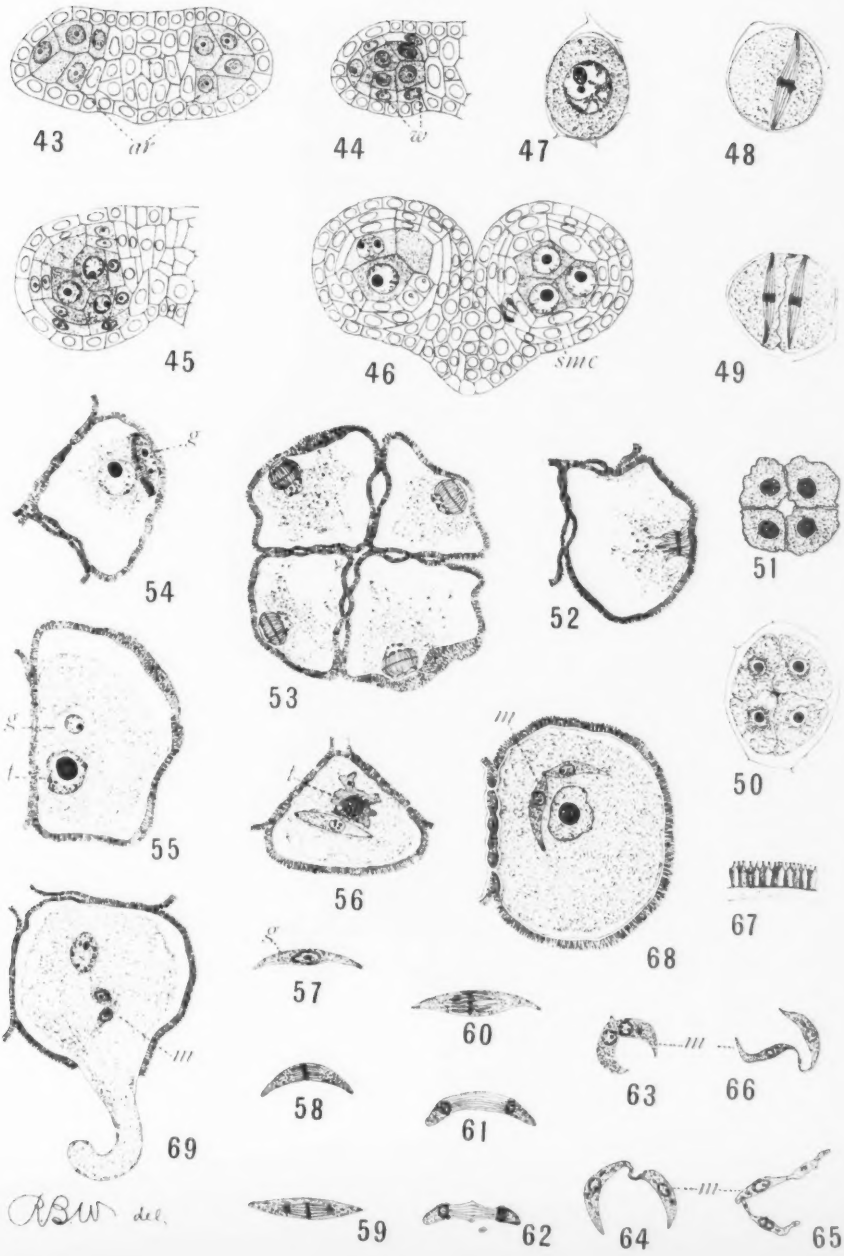
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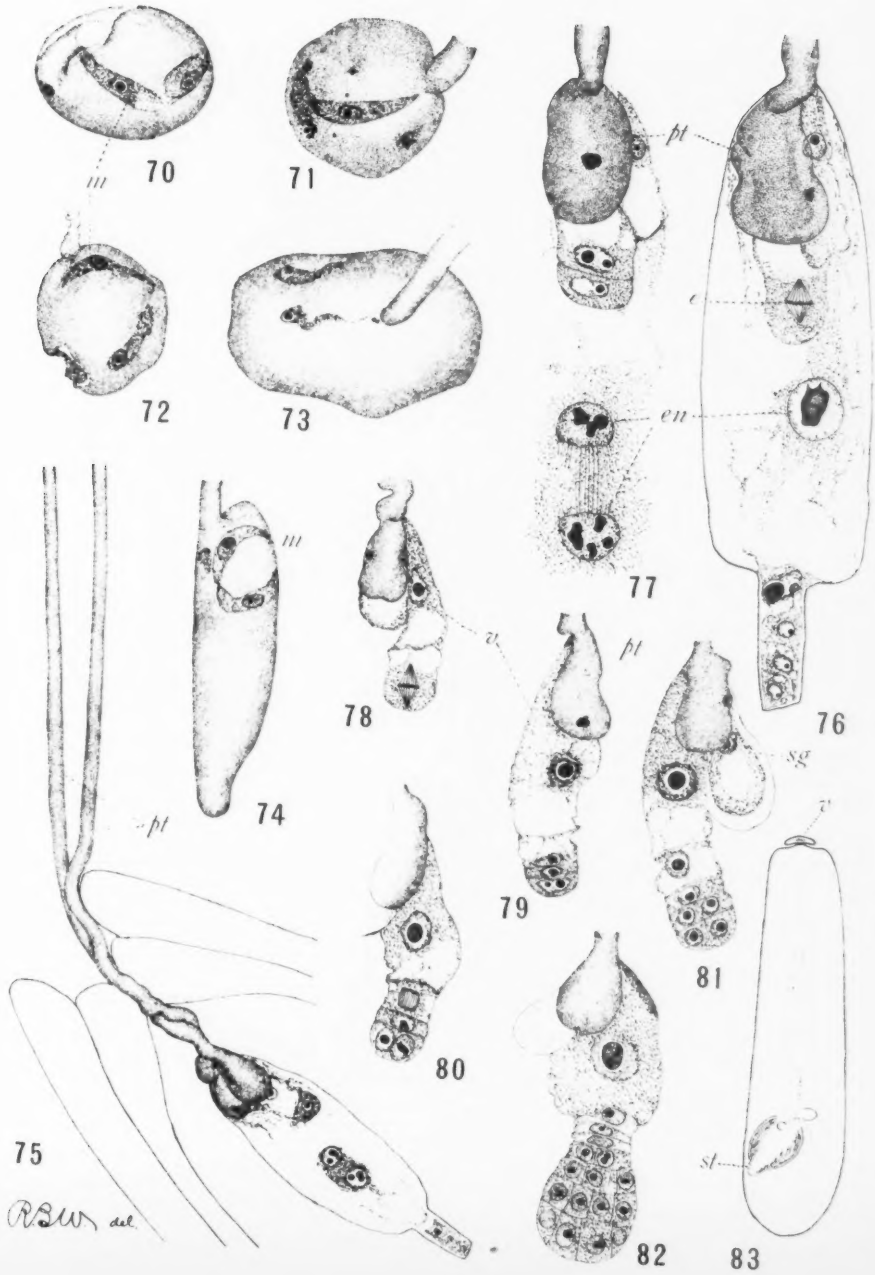
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FIG. 34. Embryo sac just before fertilization. The polars lie in contact.

FIG. 35. Embryo sac at time of fertilization. One sperm lies in contact with the endosperm nucleus; the other is uniting with the egg.

FIG. 36. A similar stage. The pollen tube contents have apparently burst out of the synergid.

FIG. 37. Antipodal group showing five nuclei.

FIG. 38. Antipodal group. The enlarged nucleus surrounded by dense cytoplasm which is bounded by a membrane.

FIG. 39. An antipodal group similar to *fig. 38* without membrane about enlarged cell.

FIG. 40. An antipodal group showing three nuclei.

FIGS. 41, 42. Polars as they lie in contact before fertilization.

PLATE III.

FIG. 43. Cross-section of stamen showing the archesporia of the two sporangia.

FIG. 44. Archesporium cutting off primary wall layer which nearly invests the primary sporogenous cells.

FIG. 45. Showing several wall layers and cells cut off the sporogenous tissue on the axial side of the sporangium.

FIG. 46. Cross-section of stamen after spore mother-cells are established.

FIG. 47. Spore mother-cell immediately before division.

FIG. 48. First division of spore mother-cell.

FIG. 49. Division of daughter-cells.

FIG. 50. Young tetrad enclosed by wall of mother-cell.

FIG. 51. Young tetrad free from wall of mother-cell.

FIG. 52. Division of microspore nucleus.

FIG. 53. Four spores of tetrad clinging together with their nuclei dividing simultaneously.

FIG. 54. Generative cell being cut off along wall of spore. The tube nucleus already enlarged.

FIG. 55. Generative cell has passed into the cytoplasm of the tube cell.

FIG. 56. Tube nucleus amoeboid in form, generative cell elongated.

FIG. 57. Generative cell as it appears before division into the male cells.

FIGS. 58–62. Stages in the division of generative cell.

FIGS. 63–66. Male cells joined in pairs by their elongated ends.

FIG. 67. The spore coats; the exine with spines.

FIG. 68. A pollen grain at time of pollination, showing tube nucleus and male cells.

FIG. 69. Pollen grain germinating on the stigma of a pistillate flower.

PLATE IV.

FIGS. 70–74. Cyst-like enlargements formed at ends of pollen tubes in ovarian cavity, showing male structures are still distinct cells.

FIG. 75. Embryo sac into which two pollen tubes have entered, showing course of tube and mode of entrance into sac.

FIG. 76. Division of fertilized egg. Endosperm nucleus still in resting condition.

FIG. 77. Division of primary endosperm nucleus in embryo sac with two-celled embryo.

FIG. 78. Two-celled embryo with lower nucleus in division.

FIG. 79. Four-celled proembryo.

FIG. 80. The end cell of embryo has divided by a vertical wall.

FIG. 81. Embryo with enlarged synergid.

FIG. 82. Later stage in development of embryo showing greatly enlarged vesicular cell.

FIG. 83. Diagram of longitudinal section of embryo from nearly ripe seed. Flattened vesicular cell at root end, lateral stem tip, and secondary roots from near base of stem.

CHEMOTROPISM OF ROOTS.[1]

FREDERICK C. NEWCOMBE and ANNA L. RHODES.

THE chemotropism of pollen tubes and of fungus hyphae and the chemotaxis of various unicellular organisms have received considerable attention in the great mass of work which has been done on the sensitive activities of plants. There is probably a well-defined notion that terrestrial roots, which are known to be hydrotropic, are also chemotropic. The unequal distribution of minerals in the soil, and of decaying organic matter, can be thought of as furnishing opportunity for the development of chemical response as a biological adaptation.

In literature there seems to be no record of work done to test the ability of roots to respond to a chemical stimulus by changing their direction of growth. This test has now been made, and the results are recorded in the following pages.

I. THE ONE-SIDED APPLICATION OF CHEMICALS IN TUBES.

The first method employed consisted in applying to the tips of roots immersed in a liquid a chemical diffusing from the open mouth of a horizontal tube.

A considerable quantity of the ordinary Sachs's culture fluid was made, containing all the ingredients except the potassium nitrate. A solution of potassium nitrate was then made of such a density that when a drop of it was placed in the solution of the other ingredients of the culture fluid, the potassium nitrate would neither rise nor fall. Rather large capillary tubes were now made, 1.5 cm long by 1 mm internal diameter and closed at one end. These tubes were then filled with the solution of potassium nitrate by the use of the air pump. Next, a row of seedlings, fastened by strips of blotting paper and rubber bands to a bar of glass, were suspended across a glass cylinder, the roots being immersed in the culture fluid containing no potassium nitrate. The tubes filled with the potassium nitrate solution were now introduced into the jar of liquid, and so adjusted that their open

[1] Contribution 68 from the Botanical Laboratory of the University of Michigan.

ends were within a few millimeters of the root-tips, there being a tube for each root. Every few hours the position of the tubes of potassium nitrate was changed in order to follow the descent of the root-tips. This method will be recognized as an adaptation of that method first employed for other purposes by Pfeffer.[2]

Altogether eighty-seven seedlings of *Helianthus annuus* L. and seventeen seedlings of *Raphanus sativus* L. were employed, for periods ranging from twenty-four to forty-eight hours at 20° to 24° C., but without showing a response. The positive curves and the negative curves were no more numerous than one might observe in these roots growing in water.

Thinking that the amount of potassium nitrate might have been too small to act as a stimulus, glass vials holding 20^{cc} were used instead. The mouths of the vials were closed by plugs of cotton previously wet with the potassium nitrate solution. Here also the roots showed no curves that could be ascribed to the chemical.

The absence of response in the foregoing experiments might be ascribed to any of several conditions. It might be that the roots used were not chemotropic, though others might be. It might be that the sunflower and the radish were chemotropic to some chemicals, but not to the potassium nitrate; though the thought suggested itself at the outset that, if roots are chemotropic they are likely to respond to chemicals which form their necessary food. It might be that the potassium nitrate was not present in large enough proportion. It might be that the difference in chemical composition was not great enough on opposite sides of the root. It might be, finally, that, while the seedling had a full supply of all kinds of stored food, it would show itself indifferent, but would respond, when it needed mineral food from without. Manifestly the thing to do was to satisfy these conditions as fully as possible.

II. THE ONE-SIDED APPLICATION OF A CHEMICAL BY DIFFUSION THROUGH A MEMBRANE.

With a view to testing the roots of plants when the food stored in the seed had been exhausted, water cultures were

[2] Ueber chemotactische Bewegungen, etc. Untersuch. Bot. Inst. Tübingen 1 : 367.

started in the plant house in a full culture solution, except for the absence of potassium nitrate. After the plants had produced secondary roots, fresh culture fluid of the same composition was exchanged for the old, and there was inserted in each jar a glass dish of solution of potassium nitrate, whose density was approximately the same as that of the other liquid, as determined by the means already described. These glass dishes of potassium nitrate, holding 30^{cc}, were closed by parchment paper, or by hardened filter paper, and the dishes were set with the membrane parallel with the main roots and 2 to 3^{mm} distant from them. The preparations were continued in the plant house for six weeks, or long after all stored food was exhausted, both fluids being renewed every ten days. The roots were shielded from the light to avoid heliotropic curving. The species used were *Raphanus sativus* L., *Fagopyrum esculentum* Moench., *Lupinus albus* L., and *Pisum sativum* L. There was, however, no chemotropism shown.

To make sure that the failure of potassium nitrate solution to act as a stimulus was not due to the relatively small quantity employed, the foregoing experiment was repeated in all its details, except that the two solutions employed were nearly equal in volume. The preparation was continued for three weeks, and the solutions were renewed in the middle of the period. The time of year was summer, and the growth was good.

It would seem as though this preparation would bring curves, if the seedlings employed were chemotropic. Here was a row of roots parallel with and within 2 or 3^{mm} of a parchment membrane 9^{cm} in diameter having different solutions on its opposite sides. It was as though the jar had been divided into halves by a parchment septum, and the roots suspended on one side close to the septum. One can hardly think that in nature conditions can be more favorable for the manifestation of chemotropism. And this preparation did show a certain response. Nine seedlings of *Lupinus albus* and forty-four of *Raphanus sativus* were used. The former showed no curves nor other response ; but the Raphanus showed a considerable number of primary and secondary roots bending toward the potassium nitrate, and a much greater

growth of lateral roots on the same side. This greater growth on the side toward the parchment membrane was not mainly due to the effect of the curving of the roots into that position; but the lateral roots on that side had made a better growth than on the opposite side. This behavior recalls the similar results obtained with varying soils by Nobbe,[3] Stohmann,[4] Höveler,[5] and Frank,[6] who obtained a greater growth of lateral roots in richer soils.

Here at last was a result indicating chemotropism of roots. Yet the method left much to be desired. With some means to insure a greater inequality in chemical composition on the opposite sides of a root, much better responses might be obtained.

III. DIFFERENT CHEMICALS BROUGHT TO OPPOSITE SIDES OF THE ROOTS BY STRIPS OF FILTER PAPER.

The device next tried was to conduct liquids of different composition to the opposite sides of the root by means of narrow strips of thin filter paper. The seedlings were suspended from a bar of glass fastened horizontally across a damp chamber. In the bottom of the chamber were placed two little dishes, one containing distilled water, the other Sachs's culture solution. From one liquid a strip of filter paper, 2 mm wide, extended upward and adhered to one side of the root, while the opposite side was covered by a strip from the other liquid. The strips of paper were not allowed to touch one another. In some tests, the small dishes were placed above the level of the root tips, and the paper strips hung downward, touching the flanks of the root-tip and then diverging and ending in dishes of water below. Every few hours the strips of paper were adjusted so as to keep them in contact with the roots near the tip. In this form of experiment nineteen seedlings of *Lupinus albus* were used, but no curves resulted. The objection to this method is found in the difficulty of keeping the paper strips in contact with the sloping sides of the root-tip.

[3] NOBBE: Landwirthsch. Versuchsstat. **4**: 222. 1862; and **10**: 100. 1868.

[4] STOHMANN: Jahresbericht über die Forschungen der Agriculturchemie 1868-69.

[5] HÖVELER: Jahrb. Wiss. Bot. **24**: 294. 1892.

[6] FRANK: Bot. Zeit. **51**: 153. 1893.

IV. THE APPLICATION OF CHEMICALS IN BLOCKS OF GELATIN.

The preceding methods all proved themselves unsatisfactory. Yet they are worth incorporating in this record, for they are methods which would probably suggest themselves to any one pursuing this subject, and it is worth while to show the unsatisfactory results they bring.

Another method was conceived which seemed to promise better control of the application of a chemical to only one side of a root. This was the employment of gelatin as a vehicle for the various chemicals. It was thought that gelatin blocks might be made with solutions of salts, and these blocks might be brought against the roots, a block on each side. There was, however, the question as to the behavior of roots growing in gelatin, and their ability to respond to stimuli. Wacker[7] determined the retardation in the growth of some roots in water, while Sachs[8] and Němec[9] mention the fact that roots inverted in air and water do not return completely to their usual geotropic position. Experiments in this laboratory have shown that there is a greater retardation of growth of roots in water than in air or earth, and a greater retardation in gelatin than in water. At the same time, it was found that geotropic response is not so great in gelatin as in water, and not so great in water as in earth or air. Still growth proceeds apparently normally in gelatin, except for retardation; and geotropic responses follow stimulation, though somewhat slowly. It was decided, therefore, to try the use of gelatin.

Large, rectangular, oblong glass jars were selected to serve as damp chambers. They were lined with filter paper, dipping into water in the bottom. Paper boxes of suitable size were then made, and these laid on glass plates, while their sides were held rigid with wooden frames. Into these boxes, as molds, the warm gelatin mass was then poured, and allowed to solidify. The gelatin mass had been made by dissolving the dry gelatin in a watery solution of the salt to be used on the roots. The

[7] WACKER: Jahrb. Wiss. Bot. **32**: 71. 1898.

[8] SACHS: Arbeiten Bot. Inst. Würzburg **1**: 409. 1873.

[9] NĚMEC: Jahrb. Wiss. Bot. **36**: 89. 1901.

gelatin blocks as they came from the molds were 15^{cm} long, 9^{cm} wide, and 2.5^{cm} thick. The seedlings to be used were fastened in the usual way to a bar of white pine which was suspended across the damp chamber at a suitable height. In the bottom of the damp chamber a glass platform had been raised above the water, and on this the gelatin blocks were laid, each block with a glass plate for a backing. A little practice soon enables one, with a hand on each glass plate, to turn the gelatin blocks up against the row of roots; and while with one hand the two blocks of gelatin are held in place, with the other hand they are secured there by bringing against the glass plate supporting them bars of wood held in place by springs of rubber tubing.

A row of thirteen seedlings of *Lupinus albus* was first used between the blocks of gelatin, one of which was made with distilled water, the other with 0.28 per cent. dry salt of di-sodic phosphate (Na_2HPO_4). The seedlings were 5^{cm} to 7^{cm} long, the temperature 23°, and the period twenty-four hours. The dry gelatin was 6 per cent. of the whole mass.

At the conclusion of the experiment, all thirteen roots were found grown into the sodium phosphate gelatin, the angles of curvature being 45° on the average. The roots looked healthy, and growth had been good. Decisive as this result was, it did not demonstrate the precise cause of the curving. The result may have been traumatropism, or hydrotropism (osmotropism), or chemotropism.

The curves could hardly be due to the presence of copper or other metal in the distilled water, for water from the same bottle was used in the gelatin on both sides of the seedlings. Yet to make doubly sure, the next gelatin blocks were made with water twice distilled in flasks of Jena glass. In this test eleven seedlings of *Lupinus albus* were employed as in the preceding experiment. Here as before all roots turned positively into the gelatin containing the sodium phosphate, nearly all angles being 45° or over.

It might be thought that the curves were due to the injurious action of the sodium phosphate on the growing zone of the root,

retarding growth there, and thus causing the tip to swing around to make the positive curve. This result would be the same as the effect of mechanically wounding a root in the elongating zone, as determined by Spalding.[10] It is to be noted, however, that to produce a positive curve by injury the sodium phosphate must act traumatically on the elongating zone, whereas we should expect it to act first on the more sensitive root apex, and produce a negative traumatropic curve. To test the relative sensitiveness of the root apex, and of the elongating zone toward a known injurious substance, a block of gelatin was made up with a 0.01 per cent. aqueous solution of crystals of copper acetate, while the gelatin used on the opposite side of the roots was made with distilled water only. Sixteen seedlings of *Lupinus albus* were used. After six hours, the temperature being 21° to 22°, the gelatin blocks were separated, and the roots were seen to be bending away from the side holding the copper salt. The gelatin was replaced and allowed to remain eighteen hours longer, when the experiment was ended. Thirteen of the sixteen roots were strongly negative toward the copper acetate, while the other three roots remained straight. All roots were living and had grown somewhat.

It is thus demonstrated that when an injurious substance is presented at the same time to both the elongating zone and the apex of a root, the negative traumatropism of the root will overcome the tendency to form a positive mechanical curve. It is thus demonstrated that the curves toward sodium phosphate in the former experiments were not traumatic.

There is still the possibility that the curves toward the sodium phosphate were due to a disturbance of the turgor of the root. The salt on the one side may have caused a shortening of the cells on that side by withdrawing water; or the low osmotic pressure of the water and the gelatin on the opposite side may have caused an inflow of water into the cells, and hence a lengthening on that side of the root.

To test the possibilities named in the foregoing paragraph, a gelatin block was made up with 3.5 per cent. watery solution of

[10] SPALDING: Traumatropism of roots. Annals of Botany **8**: 423. 1894.

cane sugar, and brought against one side of a row of roots, while the gelatin block on the opposite side was made up with distilled water. Twelve seedlings of *Lupinus albus* were used in a temperature of 22°, and the duration of the experiment was twenty-four hours. All roots grew straight.

Since in the last experiment the roots had on each side a gelatin solution of equal strength, it follows that on the side of the sugar solution there was an excess of osmotic pressure corresponding to more than 183.4^{cm} of mercury. This, however, effected no bending.

Another set of sixteen seedlings of *Lupinus albus* was set up between gelatin blocks, the one side having a 3.5 per cent. solution of cane sugar, and the other a 0.28 per cent. solution on the dry salt Na_2HPO_4. When the preparation was taken down twenty-five hours afterward, every root had grown into the sodium phosphate, the angles running from 30° to 75°.

These two experiments certainly show that the curves toward the sodium phosphate are not to be explained as osmotropism nor ascribed to any mere physical disturbance of the water content of the cells. If the curves are due neither to injury nor to the osmotic action of the sodium salt (osmotropism or hydrotropism), there remains probably but one explanation: We have here a true case of chemotropism of roots.

Accepting the foregoing results as demonstrating the positive chemotropism of the roots of *Lupinus albus* toward sodium phosphate, it would be interesting to know whether with strong solution of the same salt the root would show itself negatively chemotropic.

A row of ten seedlings, having on one side a gelatin block made with distilled water, and on the other side a block made with 2 per cent. dry salt of di-sodic phosphate, had all their roots killed within a few hours. Another row of ten seedlings, similarly treated except that the gelatin on one side was made up with a 1.5 per cent. solution of the sodium salt, showed, after twenty-four hours, all the roots bent into the gelatin containing the chemical. All of the roots except one were dead. All had grown sufficiently, however, to make the curve before dying.

A third row of ten seedlings of the same species, set up between gelatin and distilled water on one side and gelatin and 1 per cent. di-sodic phosphate on the other, gave eight roots bent into the gelatin containing the chemical, while the other two roots were straight. None of the roots were dead. In the twenty-four hours of the last experiment, the roots had grown but about 10^{mm}, though the temperature was 20° to 23°. This shows a retardation of growth to about 50 per cent. of what it would have been in air or soil.

The last series of three experiments demonstrates that by strong solutions of sodium phosphate the roots of this plant unable to turn in negative chemotropism are helplessly lured on to certain death. The case is similar to that of several free-swimming organisms, mentioned by Rothert[11], which swim into solutions of lethal osmotic strength.

Though the roots of *Lupinus albus* are positively chemotropic toward di-sodic phosphate, they do not display a like behavior toward all salts that are absorbed by plants as food. Seedlings of *Lupinus albus* to the number of thirty-seven suspended between blocks of 5 per cent. gelatin, one block holding only distilled water, and the opposing one a 0.5 per cent. solution on the anhydrous nitrate of ammonium, showed when the preparations were taken down twenty-four of the roots grown into the block containing no chemical, while the other thirteen roots were straight.

A similar preparation with the same species was made with gelatin with distilled water on one side, and with gelatin and a 0.75 per cent. solution of water-free calcium nitrate on the other side. At the end of the experiment twenty roots were negative toward the salt, and the other eight roots were straight. Still another set of seedlings of the same species was prepared with roots between gelatin and distilled water on one side and gelatin and a 0.375 per cent. solution of the water-free calcium nitrate on the other. The result turned out as before, except that a smaller proportion of roots bent. Of the seventeen roots, eight

[11] ROTHERT: Beobachtungen und Betrachtungen über tactische Reizerscheinungen. Flora **88**: 409. 1901.

turned into the gelatin holding distilled water only, while nine grew straight.

Used in experiments similar to the foregoing, a 0.5 per cent. solution of potassium nitrate caused nine roots of the lupin out of ten to turn slightly into the distilled water gelatin, while the tenth root bent into the potassium nitrate gelatin. The growth was good, the roots not distorted, and the curves were slight. A 0.6 per cent. solution of anhydrous magnesium sulfate caused very slight curvatures in the lupin roots, but all ten roots certainly bent into the distilled water gelatin.

The curves described above as following the use of ammonium nitrate, calcium nitrate, potassium nitrate, and magnesium sulfate may have been either negatively traumatropic or negatively chemotropic. In view of the behavior of the roots of this plant toward gelatin containing 3.5 per cent. of cane sugar, the curves last described could not have been osmotropic. The experiments certainly do show that *Lupinus albus* is not similarly chemotropically sensitive to all salts that it may absorb as food. Its roots are positive toward all solutions of sodium phosphate tried, but they turn away from solutions of corresponding osmotic strength of the other salts used.

During the course of the work it seemed of interest to test the behavior of the roots of the lupin when two unlike salts of the same osmotic pressure were brought at the same time against opposite sides of the roots. For this purpose isosmotic solutions were made of potassium nitrate (KNO_3), calcium nitrate ($Ca(NO_3)_2$), and magnesium sulphate ($MgSO_4$). The solutions were made by the specific gravity method to give a pressure equal to 130^{cm} of mercury, it being assumed that in these weak solutions ionization was complete. It was assumed also that KNO_3 gave two ions, $Ca(NO_3)_2$ three ions, and $MgSO_4$ two ions.

When these isosmotic solutions of potassium nitrate and of calcium nitrate were opposed on the flanks of a row of lupin roots, nine of the eleven roots grew into the potassium nitrate, two roots growing straight. When potassium nitrate and magnesium sulfate were opposed, ten of the eleven roots grew into the potassium salt, and one into the magnesium. When calcium

nitrate and magnesium sulfate were opposed, ten of the fourteen roots grew into the magnesium salt, while the other four roots remained neutral.

When we remember that all of the four salts last used caused the lupin roots to bend negatively when these salts were severally opposed to distilled water gelatin, we may be certain the curves noted in the preceding paragraph were repulsion and not attraction curves. The magnesium sulfate therefore repels more strongly than the potassium nitrate, and the calcium nitrate more strongly than either the potassium nitrate or the magnesium sulfate. Whether this repulsion is chemotropic or traumatropic cannot be decided at this time.

To ascertain whether other plants are chemotropically sensitive as *Lupinus albus* has been found to be, seedlings of *Cucurbita Pepo* L. have been put to the test.

Isosmotic solutions of potassium nitrate, calcium nitrate, and magnesium sulfate were prepared with computed pressures equal to 130^{cm} of mercury at a temperature of 15°. With these solutions blocks of gelatin (6 to 10 per cent. of gelatin according to the general atmospheric temperature) were made up and brought against the roots of the seedlings suspended in rows in damp chambers. The results may be shown in tabular form, the chemicals in a horizontal row being in opposing blocks of gelatin, the column of figures to the left indicating the number of roots curving toward the salts to the left, the figures in the middle column indicating the neutral roots, and the figures at the right indicating the number of roots curving toward the salts there given.

		Curved	Neutral	Curved		
KNO_3	–	1	9	0	→	$MgSO_4$
KNO_3	"	2	16	10	"	$Ca(NO_3)_2$
$MgSO_4$	"	0	9	3	"	$Ca(NO_3)_2$

Through an error in reading the specific gravities of solutions as given in Gerlach's tables,[12] the stock solution of di-sodic phosphate was made with an osmotic pressure of 39^{cm} of mercury, instead of the same pressure as the solutions of the three salts

[12] Zeitsch. Analyt. Chemie **8**: —. 1869.

last used. Before the error was discovered, *Cucurbita Pepo* had been tested as shown in the following table, the explanation of the columns of figures being the same as for the preceding table, and the salts held in gelatin blocks as before.

		Curved	Neutral	Curved		
KNO_3	←	3	19	7	→	Na_2HPO_4
$Ca(NO_3)_2$	"	2	9	1	"	Na_2HPO_4
$MgSO_4$	"	0	8	0	"	Na_2HPO_4

It is probable that the results would have been approximately the same in the last table if the solutions of salts on the opposite sides of the roots had been osmotically equal. *Lupinus albus* was tested in precisely the same way and with the same chemicals as given in this table, and the result showed thirty roots out of thirty-seven curved toward the sodic salt, and not one root curved toward the three other chemicals.

From the two foregoing tables, this result certainly stands out: *Cucurbita Pepo* is neither attracted nor repelled by the chemicals used as is *Lupinus albus*. If its direction of growth is controlled at all, it is but feebly so by the di-sodic phosphate and the calcic nitrate; but it is more probable that it is not chemotropic, at least toward the salts here used, and that the curves that came were due to disturbances of growth, not falling within the realm of chemotropism.

CONCLUSIONS.

The experimental results recorded in the foregoing pages show that the roots of *Lupinus albus* are chemotropically positive toward solutions of di-sodic phosphate, and that no concentration of solution of this salt will produce a negative curve. The stronger solutions used (1.5 per cent.), cause first a curving toward the salt and then death. The death of the roots in such a solution may be due to the osmotic strength of the surrounding medium. The osmotic strength of the salt solution plus that of the gelatin probably amounts to somewhat more than four atmospheres of pressure, and such a pressure is probably greater than that of the cells of the distal millimeter of the root-tip.[13]

[13] STANGE: Bot. Zeit. **50**: 292. 1892.

The particular attractive component of the salt is not shown. It may be either the sodium or the phosphoric acid ion. Recalling the work of Stange[14] and of Buller[15] one might think the response to be due to the PO_4 ion. Experiments now being made in this laboratory will, it is hoped, determine this question.

The general indifference of the roots of *Cucurbita Pepo* toward the chemicals used indicates that we may expect further study of the chemotropism of roots to show the same specific differences in sensitiveness to chemicals as is shown in sensitiveness toward light; that is, there will be found chemotropic and non-chemotropic roots.

The behavior of all the roots tested gives no indication of osmotropism. *Lupinus albus* was indifferent to the one-sided application of a 3.5 per cent. solution of cane sugar, and the same plant gave no negative bends when a solution of the di-sodic phosphate concentrated enough (four atmospheres) to cause death was applied to one side only. Yet the roots of this plant are hydrotropic. The roots of *Cucurbita Pepo* were indifferent when chemicals plus the gelatin gave osmotic pressure of about 78^{cm} of the mercury on one side and 170^{cm} of mercury on the other.

From Rothert's[16] view one would regard osmotropism and hydrotropism as identical; yet it is not improbable that roots will be found which are not osmotropic though they are hydrotropic. Such is the indication in these experiments.

The behavior of the lupin roots in curving away from all chemicals used except the sodic salt, may be either traumatropic or chemotropic. Or may this not be a reaction where chemotropism and traumatropism lose their distinction?

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[14] STANGE: Bot. Zeit. **48**: 124. 1890.

[15] BULLER: Annals of Botany **14**: 558. 1900.

[16] ROTHERT: Flora **88**: 415. 1901.

BOTANICAL SURVEY OF THE HURON RIVER VALLEY.

II. A PEAT BOG AND MORAINAL LAKE.[1]

LEWIS H. WELD.

(WITH SIX FIGURES)

WHILE the general history of morainal lakes and the superficial relations of their plant societies have long been familiar both to botanists and geologists, there has been great lack of detailed information regarding changes now taking place and the effects of such changes on the distribution of plants and consequent vegetable accumulations. In fact, anything approaching a satisfactory comparative study, based on reasonably complete data, has thus far been out of the question. The evidence goes to show that the rate at which morainal lakes in southern Michigan are filling up has been extremely variable and that oscillations of water level and various other changes are in progress, directly affecting biological conditions. For future critical studies, therefore, it is essential that definite observations of present conditions should be permanently recorded. The large number of morainal lakes in the Huron River Valley and the numerous peat bogs accompanying them, some of which are reported to be as much as forty feet in thickness, offer excellent opportunity for scientific exploration and commercial enterprise to cooperate with mutual advantage.

The lake, or pond, which forms the subject of the present study, is the first and smallest of the so-called Three Sister Lakes, and lies three miles west of Ann Arbor, just south of the trolley line. It is oval, or ovate, in outline, with the long axis SSW by NNE, the larger end lying towards the south. Its greatest length is 600^{ft} (180^{m}) and its width 400^{ft} (120^{m}); on the west

[1] This work, to which Mr. Weld gave a large part of his time for a year, was incomplete when he left the University of Michigan in July 1902. As the work was carefully done, it seems desirable to place his observations on record. With his approval, some necessary changes and additions have been made by V. M. Spalding, under whose direction the survey is in progress.

is a strip of tamarack swamp and low ground several acres in extent, through which flows to the southwest the outlet, a mere ditch, dry except in spring. Across the road, north of the present lake, is a small marsh, part of the same basin, cut off in the early days by a corduroy road and now by the high embankment of the trolley line. It had no drainage to the north. The general

FIG. 1.—First lake from the N. W. on the trolley embankment.

relations are shown in the view from the trolley embankment (*fig. 1*).

About 1200^{ft} (365^{m}) to the south lies a second lake, larger and nearly circular in outline, hemmed in except on the north and northwest by badly eroded hills. Its outlet is a ditch on the north side, which joins the outlet from the first, then flows straight west, crossing the road, through a low marsh, nearly to the woods beyond, and then turns to the northwest. West of the second, a quarter of a mile away, is the third lake, the lar-

gest and deepest of the group. It is not connected with the other two, a low, gravelly ridge separating it from the marsh just east of the woods, through which the other outlet flows. The outlet of this third lake flows through a bog at its western extremity, then to the southwest, where it makes a great bend through a level plain; then, after two or three miles, it turns north again, joining the outlet of the other two and forming a branch of Honey Creek which empties into the Huron River about a mile above Foster's.

The levels of these lakes are approximately the same, *i. e.*, 914^{ft} (278^{m}) above sea level or 33^{ft} (10^{m}) above the bench-mark on the library building of the State University, and 120^{ft} (36.5^{m}) above the Huron River at the outlet of Honey Creek. The summit of the divide east of the first lake is 955^{ft} (291^{m}) above the sea, or 41^{ft} (12.5^{m}) above the lakes. The corner on Liberty Street, one mile south of Huron is 979^{ft} (298^{m}) and the kame just south of Liberty Street rises probably 75^{ft} (23^{m}) higher. It was once proposed to derive the water-supply of Ann Arbor from the third lake, pumping the water to a reservoir on top of this kame, about 140^{ft} (42^{m}) above the lake.

Ordinarily the level of the three lakes remains nearly constant throughout the year, becoming, however, 6 to 8^{in} (15–20^{cm}) higher in the spring. In the fall of 1901 the lakes were said to be lower than they had been in years. It is popularly supposed that they are fed by springs, but careful testing with a thermometer, in the fall of the year, has thus far failed to detect the influence of such springs. It is a very common thing, however, for lakes of this sort to be sub-irrigated, that is, water percolating through the stony clay of adjacent hills makes its way to the lake, and, owing to the higher water-table on all sides, maintains the level constant in the lake basin. Another thing which helps to retain the water is the fact that the bottom of the lake basin is filled with a deposit of blue clay which prevents leaching. The depth of the lakes varies with the size, the first being 18^{ft} (5.5^{m}) deep, the second over 35^{ft} (10.5^{m}), and the third 55^{ft} (16.75^{m}).

This group of lakes is of glacial origin, like numerous other

small lakes of Michigan. They lie on the western slope of the terminal moraine which was formed by the Erie lobe of the ice sheet, and which now extends northeast and southwest across the county. Just south of the second and third lakes is a high kame, and these lakes lie in some of those local depressions in the drift which are characteristic of a kame area. The present outlets follow the glacial drainage channels. These flowed away from the ice front to the north and northwest to the Huron River, which at that time had just formed in the re-entrant angle between the Erie and Saginaw lobes and flowed to the west through the Portage and Grand into Lake Michigan. All the region east of this terminal moraine, including Ann Arbor, was then occupied by the ice sheet, and the glacial drainage was to the west.

As is well known, such morainal lakes are destined sooner or later to become obliterated by the combined action of erosion and vegetation. The process goes on more slowly in some than in others, depending on size, depth, character of the shores, direction of winds, and the nature of the vegetation which gets a foothold. The first lake represents a fairly advanced stage in the process, the second and third occupying a far larger proportion of their original basins.

The characteristic zonal distribution of the vegetation is well marked in all three of these basins, especially in those of the first and third, the lake lying in the center with water lilies around its margin, then sedge and sphagnum, cassandra and other shrubs, and finally forest. It is noteworthy that the lake, as in many similar cases, is nearer the eastern than the western side of its basin, the bog and forest being better developed on the western side. This is not so evident in younger stages, but is very noticeable at the first lake.

Proceeding now to a more detailed account of the vegetation of the first lake, we may conveniently follow the zones in their natural order:

1. *Potamogeton zone.*—This is represented by *Potamogeton lucens*[2] in deep water, at the outer edge of the pond lilies, not at

[2] The nomenclature is that of Gray's Manual.

all abundant, and by *P. zosteraefolius*, which is also sparingly present. The open water is 18ft (5.4m) deep in the deepest place, which is near the south end. The bottom is of blue clay with a very thin film of black organic matter resting upon it. This clay bottom is derived from eroded material that has washed into the lake, chiefly before so much peat had accumulated around the borders of the basin, the finest of which, in turn, has been washed out into the middle of the lake and has settled in the deepest water. A section of the lake opposite the ice-house (*fig. 2*) shows that it is a flat-bottomed, saucer-shaped basin.

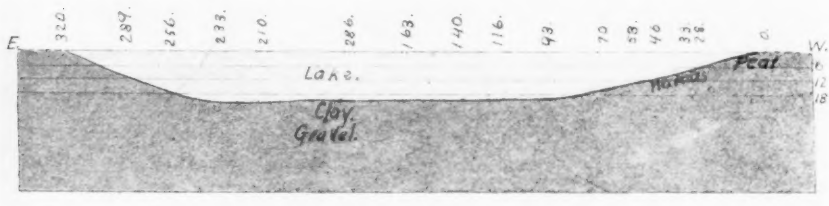

FIG. 2.—Section through lake opposite ice-house. Scale 1:900.

As we approach within 50 to 60ft (15–18m) of the shore we come to the rather steep incline of the terrace formed by the border vegetation. This is composed of dead organic material in which sphagnum is conspicuous. Even though the lake is small, the waves probably stir it to the bottom, as it is so shallow. The water is highly colored, a yellowish-brown, by the decaying organic substances, and contains much solid matter in suspension.

2. *Nuphar zone*. The terrace just described is occupied by a very prominent and almost unbroken zone of yellow pond lilies from 20 to 30ft (6–9m) wide, growing in water from 6in to 5.5ft (15–167cm) deep. It is widest in the quiet water of the southwest end of the lake, while on the east there are a few short spaces where it is interrupted altogether; but on the whole it is an almost perfect zone. These lilies are most efficient agents in reclaiming a lake. Not only can they creep out with their stout rootstocks into 6ft (2m) or more of water, binding together

the humus and contributing to it by their own decay, but their long petioles and large leaves break the force of the waves so that in the quiet water thus afforded a variety of less resistant forms can grow, adding the products of their decomposition to that of the lilies and to the débris which they collect.

The plants found growing here in the lily zone are :

Nuphar advena, giving character to the zone and preferring shallower and more quiet water than the next; Nymphaea odorata, in two isolated patches only, as if recently introduced; Brasenia peltata, replacing the lilies in two places; Potamogeton natans, a few specimens; Ceratophyllum demersum, scattering, not in dense beds; Utricularia sp., close to shore not abundant; Chara sp., two flourishing clumps near shore, each about a foot square, apparently recently introduced; Naias flexilis.

This zone then is made up almost wholly of Nuphar, which is replaced in spots by Nymphaea or Brasenia, while a very small number of other plants, represented by few individuals, grow on the soft, black, almost bare bottom. It would seem, therefore, that the yellow pond lily is an agent of prime importance in forming the soil in which various plants named in the following sections flourish. The relative importance of species in this and succeeding zones in the formation of peat should be investigated.

3. *Carex and sphagnum zone.* This is separated from the lily zone by a distinct though irregular line of demarcation. It presents a low, level appearance, being formed in great part of grasses and sedges uninterrupted by taller plants or shrubs (*fig. 3*). Its flora, however, is varied, consisting of about thirty species. Carex, with some six species, predominates; and, with several grasses, ferns, and other plants, forms a thick, tough, flexible mat resting on water or liquid mud beneath. This zone is less distinctly defined and the mat less compact, and hence less safe to walk upon, on the eastern than on the western side. Ordinarily, however, it will hold a man's weight clear to the edge, even when the water is high in the spring, without breaking. Some species of plants prefer the lakeward border, growing at or near the water's edge; among these are the sensitive and flowering ferns, swamp milkweed, Dulichium, Eleocharis, and certain other sedges, besides seedlings of Bidens and a mint, evi-

FIG. 3.—Zone of sedges. Taken at south end of lake, looking S. W.

dently from seeds that have floated to the places where they are growing. Others grow further back, among which are the cranberry, buck-bean, white violet, and sphagnum. Following is a list of the plants of this zone, as far as determined, somewhat in the order of their relative importance and abundance.

Carex filiformis, Glyceria nervata, Eleocharis palustris, Aspidium noveboracense, Viola blanda, Menyanthes trifoliata, Potentilla palustris, Equisetum limosum, on east side near edge of water, Vaccinium Oxycoccus on S. E. and N. W., Carex four species, Onoclea sensibilis, Osmunda regalis, Asclepias incarnata, Dulichium spathaceum, Eupatorium perfoliatum, Mentha canadensis, many seedlings of Bidens and Impatiens in spring, Cassandra calyculata, Salix myrtilloides, Eriophorum gracile, Scutellaria galericulata, Campanula aparinoides.

At the north end of the lake, in a particularly soft place, is a patch of *Typha latifolia*, but elsewhere there is a sharp transition between lilies and sedges, the Pontederia and Typha zones as commonly represented being wanting at this lake.

4. *Cassandra zone*. This zone is characterized by an advance of shrubs, of which cassandra is the most conspicuous. This, with the accompanying sphagnum, is active in raising the marsh and preparing it for tree growth (*fig. 4*). It is not present in all cases, but when present the succeeding forest floor is much drier. Its development here is weak. It is accompanied by Andromeda, chokeberry, small willows, huckleberry, low birch, and mountain holly. Around some lakes east of Whitmore this zone of shrubs is much better developed, consisting, however, of willows as dominant species, with no cassandra.

The plants of this zone at the first lake include: Cassandra calyculata, Sphagnum sp., Andromeda polifolia, Pyrus arbutifolia melanocarpa, Nemopanthes fascicularis, Gaylussacia resinosa, Salix myrtilloides, Viola blanda, Rumex Acetosella in the drier spots, Lycopus lucidus americanus, Glyceria nervata, Aspidium noveboracense, Osmunda cinnamomea, Solidago sp., Sarracenia purpurea growing half hidden in the sphagnum at the base of the clumps of cassandra, Drosera rotundifolia between clumps of cassandra with sphagnum and buck-bean at the northwest side of the lake, Arethusa bulbosa growing in the sphagnum, Habenaria lacera, Pogonia ophioglossoides, Calopogon pulchellus, Menyanthes trifoliata.

We are still at a loss to explain the distribution of these bog plants, particularly the orchids.

FIG. 4.—Young tamaracks; cassandra underneath.

5. *Forest.* Next comes the only tree that seems to be able to endure these conditions, the tamaracks, small ones advancing into the cassandra zone, in one instance even within 6^{ft} (1.8^{m}) of the water and farther back larger trees 12–16^{in} (30–40^{cm}) in diameter (*fig. 4*). This forms a forest of one species of tree, constituting the grove west of the lake. There the trees stand close together, and the shrub vegetation, cassandra in particular, is killed by lack of light. The forest floor is covered with dead brown needles, with only the occasional green of a moss, sedge, fern, or composite pushing through between the clumps of dead cassandra. This is one type of bottom vegetation in a pure tamarack woods. Where the growth of tamaracks is more open, particularly if the ground is rather wet, a great variety of leafy herbaceous undergrowth completely covers the ground. This is the case in a swamp near Cavenaugh Lake, where under the scattered tamaracks there is a rank growth of skunk cabbage, indian turnip, ferns, woodbine, grape, vervain, mints, elder, and juniper. In this case cassandra had not been present in the basin to dry the bottom. Another swamp near Whitmore, consisting of small trees close together, was found to be very wet, the roots of the trees creeping on top of the ground and densely covered with sphagnum, little else being present. No cassandra had been there.

Into the pure tamarack forest at the first Sister Lake, where the conditions permit, namely in the grove on the northwest, the following are now coming in :

Prunus serotina, Acer dasycarpum, Populus tremuloides, Rhus glabra, Quercus rubra, Rubus villosus, Osmunda cinnamomea, O. regalis, Pteris aquilina.

Leaving the basin level and the forest and going up hill on the west side, we pass to ground that has been cultivated, now in meadow. A few feet up the hillside we come to a distinct zone of white vervain, about 10^{ft} (3^{m}) wide, which winds around the foot of the hill, its position evidently determined by water supply.

The succession of plant societies as here described, which is ideally perfect on the north and northwest, has been modified

elsewhere by conditions induced by human agency. Thus the area east of the lake, beyond the line fence, is characterized by an absence of forest and a scanty development of shrubs, though tamaracks once stood there within the memory of old settlers, and the stumps are still present. After they were cut, continued pasturing prevented their coming in again and favored the development of sod. West of the fence, however, where stock has been excluded, there is a good development of both trees and shrubs, and no sod has been formed. South of the ditch to the west of the lake the tamaracks were cut off, perhaps fifteen years ago, and cassandra and other shrubs have come in, with a multitude of young tamaracks which will eventually kill out the cassandra. A portion of this area, where the tamaracks were cut, was burned over in or near 1890. Following the burning, a dense growth of Marchantia covered the ground, but it has all disappeared since, and the ground is now occupied by

Populus tremuloides, Populus grandidentata, Salix rostrata, S. lucida, S. amygdaloides, S. cordata × sericea?, Pyrus arbutifolia melanocarpa, Acer dasycarpum, Cornus stolonifera, Larix americana, Rubus villosus, R. strigosus, Rhus glabra, Pteris aquilina, Osmunda cinnamomea, O. regalis, Poa pratensis, Eupatorium perfoliatum, Typha latifolia, and other species, constituting a swamp clearing society. Occupation by a much wider range of species is possible and often occurs.[3]

The general topography and the extent of the vegetable deposits show at a glance that this lake was once much larger and its level some higher than at present. By digging a series of holes in the basin through the peat the bottom contour of the old lake is seen to conform to the present contour of the surrounding hills. It is thus found that the old lake included the marsh north of the road, for a boring in the road near the sluice shows 2 ft (61 cm) of till, washed in and brought in to build the road, and below that 7 ft (2.1 m) of peat. A series of borings 100 ft (30 m) apart (*fig. 5*) shows that to the east of the line fence the lake was comparatively shallow, shown by the 8 to 9 ft (2.4–2.7 m) of peat, with a gently sloping bank on the eastern side, as would be expected from the contour of the present hill.

[3] The above lists were made in spring, and accordingly include few composites. The attempt has been made to give representative lists rather than complete ones.

West of the fence, however, the peat is over 20 ft (6 m) thick, and here was a deep part of the lake. In a few of these borings an attempt was made to determine the thickness of the blue clay, but there is no sharp separation between the clay and the gravel beneath. *Figure 6* shows a cross section of the basin in an east and west line through the north end of the lake. The western slope was not so steep at this place and the lake was more disk-shaped. How much deeper than 20 ft the peat may be in places near the lake has not been ascertained.

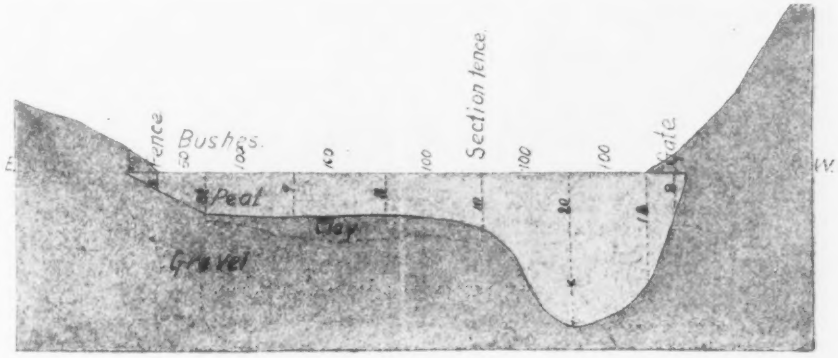

FIG. 5.—Section across lake basin from E. to W., halfway between lake and road, in line with fence. Hor. scale 1 : 2160; vert. scale 1 : 360.

Directly south of the lake is a shallow valley leading over to the second lake. A boring in the bottom of this at the fence shows 8 ft (2.4 m) of gravelly clay mixed with dark organic materials. This valley was once quite deep and formed a connection between the lakes, but being narrow was filled up by erosion rather than by vegetable deposits. West of this valley is a hill now under cultivation, and to the west of this is a broad valley in which runs the present outlet of both lakes. The peat in this valley is over 16 ft (5 m) deep, showing that here was a broad and deep connection with the second lake, the hill being at that time an island.

The Three Sisters were then originally two lakes, the third,

which has always been separate, and one from which the first and second and the marsh north of the road have been derived. The original lakes were some 5 to 6ft (1.5–1.8m) higher than at present, as is shown by a beach or terrace north of the second lake, and by other evidence. Their lowering is apparently due in great part to better drainage since open ditches have been cut in the outlet channels.

It is very desirable that a complete enumeration and comparison of the fauna and flora of the first and second lakes should be made. Here are two lakes that once were one, but except for the connection through a ditch running only in the spring, have been isolated for a long period. The physical characteristics of the two lakes are now very different, and, assuming that they were both inhabited by the same forms when there was one uniform condition, it would be reasonable nevertheless to expect modifications or variations to arise, particularly in the aquatic life, following the changes in external conditions. Some differences in the present plant life of the two lakes are now very noticeable, the phytoplankton of the first being very different from that of the second. The latter contains an enormous number of blue-green algae, Oscillaria and others, or at least did all through the winter and spring, while the first lake had none. Desmids appeared in great abundance in a culture dish from the first lake, while the other gave few. More diatoms have been present in the second lake than in the first. The second contains many Volvox, not found at all in the first, and some Eudorina. Two representatives of the Peridineae, *Peridinium tabulatum* Ehrh. and *Ceratium hirudinella* O. F. Müller, occur in each lake. The paucity of higher plants is noticeable. The first lake has no Elodea or Myriophyllum, only three species of Potamogeton, little Ceratophyllum, and but two small clumps of Chara. The flora of the second lake, not yet sufficiently studied, is apparently quite as scanty. The presence or absence of flowering plants seems to be largely a matter of the chances of dispersal, but this certainly does not account for the differences in the phytoplankton of the two lakes. In seeking an explanation of this account must be made of their

physical differences, among which the following are to be specially considered:

1. *Color.* The water of the second lake is clear, or would be if the blue-green algae were filtered out, while that of the first is highly colored, a yellowish-brown, due to the great amount of decomposed vegetable substances about the lake. This latter fact is the greatest difference between the two lakes, perhaps the cause of all others, but there is as yet no wholly satisfactory explanation of the antecedent fact that something like 95 per

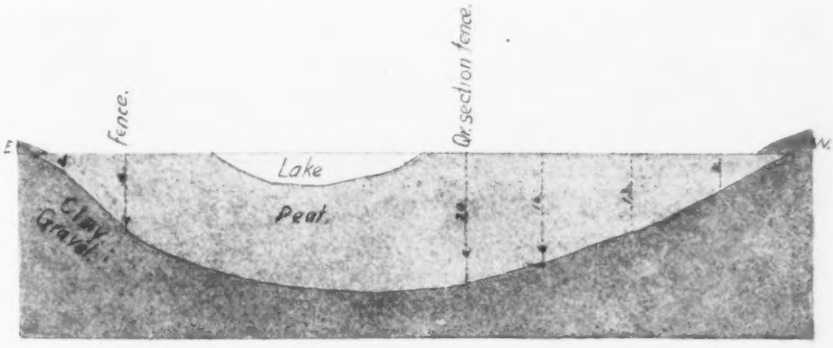

FIG. 6.—Section across lake basin from E. to W. at ditch. Scale as in *fig. 5*.

cent. of the work of filling one basin has already been done, while the process is but fairly started in the other. The greater depth of the second may have something to do with this. The ice in the first lake is clear as crystal. Freezing in winter and evaporation in summer serves to concentrate the amount of dissolved salts in the water and thus still further deepen the color.

2. *Turbidity.* Absorption of light, as is well known, is much greater in colored than in clear water, and it is also occasioned by turbidity due to the presence of solid matter in suspension. Turbidity is most conveniently measured in the field by the wire method of Hazen, which consists in observing the depth at which a platinum wire 1^{mm} in diameter disappears when lowered horizontally into the water. The scale is furnished by the recip-

rocal of the depth in inches at which the wire becomes invisible. As recently modified by Whipple and Jackson, turbidities are read directly from the scale as parts by weight of suspended matter in a million of water, making this a very simple observation and worthy the attention of botanists engaged in the study of aquatics. November 12, 1902, a reading of 11.5 was obtained. No readings were taken on the second lake.

3. *Temperature.* This, coupled with depth, may account for periodic phenomena observable particularly in the case of diatoms. The first lake is so shallow that stagnation never occurs. The bottom is a little more than a degree cooler than the surface. The second lake is over 35^{ft} (10.6^{m}) deep in places, and, though no temperature readings have yet been taken, stagnation may occur, causing at the time of the spring and fall overturning an increase in the diatom flora. At all events the second lake showed many limnetic diatoms in the spring, more than in May, leading to the inference that stagnation does occur.

The chemical composition of the water, which may be the determining factor for the presence of blue-green algae in one lake and their absence from the other, has not yet been examined.

The facts here presented show plainly that the history of these morainal lakes, as regards their vegetation, is by no means identical. Differences of depth and contour, of soil and drainage, of water supply and the chances of seed dispersal, with other less conspicuous factors, have resulted in great differences in the rate of filling up and in the character of their plant life. The first lake stands as a representative of a large number in this valley that show essentially the same succession of plant societies. After the retreat of the ice the ground could hardly have been left bare for any considerable period. If this had been the case, the evidence would be seen in much greater erosion than has actually taken place. As it is, these areas, held by vegetation, show the even curves of ice- and water-formed topography. We are to think of forest-covered hills surrounding a newly formed lake basin. Aquatics and amphibious plants are already growing about its edge, and as the humus accumulates, sedges, bushes, and finally trees follow. As the basin becomes filled up with

peat the lake first disappears from the center, then the bog, and so on until a tamarack woods fills the basin. Into this pure growth of tamarack there come in slowly elm, ash, maple, birch, basswood, and their accompanying undergrowth. A swamp near Cavenaugh Lake was observed where elms and ash a foot and a half in diameter had come in, overtopped the tamaracks, and killed them. This swamp had a very leafy undergrowth. Thus the final stage is a damp, rich-woods flora of soft woods; never does a hard-wood flora take possession, as far as my observations in this region extend, although an occasional oak or juniper may be found.

The history just outlined has been greatly modified in individual cases, as the remarkable differences between the first and second lakes plainly show, and future investigations should take full account of such differences. Thus far, critical comparisons of the flora of different lakes and bogs and the conditions affecting their plant life are wanting. The distribution of their phytoplankton presents many unexplained facts, and the factors determining the peculiarities of bog xerophytes are still an unsolved riddle. The deposition of peat is progressing with varying rapidity in numerous bogs and swamps in southern Michigan, but the processes involved in its formation and affecting not merely its fuel value but its fitness for further plant growth, and hence the composition of succeeding plant societies, are still very imperfectly known. The valley of the Huron River, with its great number of lakes and variety of conditions, offers a favorable area for more extended study of these problems.

SUMMARY.

1. These lakes were formed in the moraine at the front of the ice sheet when the Erie lobe extended 3 miles (5^{km}) west of Ann Arbor. The present outlets follow the glacial drainage to the west into the Huron River, which then flowed west into Lake Michigan.

2. The third lake never was connected with the others. The first and second were once one, with an island in the center. Subsequent lowering of water and filling of channels has made two lakes.

3. Since their separation the physical characters of the two lakes have become very different, leading to marked differences in the character of their plankton.

4. These differences appear to be due primarily to the greater depth of the second and the more rapid filling of the basin of the first lake. The reasons for the latter are not clear.

5. A luxuriant flora probably flourished on the terminal moraine at the time of retreat of the ice sheet. The lake was first invaded by aquatic and amphibious plants. As humus accumulated, there followed in turn sedges and sphagnum, shrubs, a pure tamarack, and then a mixed, soft-wood, deciduous forest.

6. Vegetation accumulated faster on the western than on the eastern side of the lake, due at least in part to the direction of prevailing winds. The ax, fire, and pasturage have obscured the order of succession in some places and prolonged the period required for the ultimate reclamation of the basin. Other causes, not yet sufficiently investigated, have resulted in marked differences in composition of the bog floras of this and neighboring lakes, and in the constitution and rapidity of formation of the vegetable substances with which they are becoming filled.

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SOUTHWESTERN PLANTS.

LESLIE N. GOODDING.

EARLY in the season of 1902 the writer visited the southern part of Nevada and Utah for the purpose of securing as large a representation of the flora as possible. On arriving at Calientes, the extreme southern point of the Oregon Short Line at that time, in the latter part of April, it was found that the plants were not yet in condition to collect. On that account the trip was extended southward along Meadow Valley Wash, the Muddy, and the Virgin to the Colorado River. From thence return was made along the Virgin to St. George, Utah, and directly across to Modena, Utah. Calientes was again visited and collections made of plants that had now come into condition. Returning northward through Utah, stops were made at every convenient point on the railroad, from which visits were made to some of the desert portions of central Utah and to several localities in the Wasatch Mountains. Leaving the railroad at Carter, Wyoming, with camp outfit, and traveling southward, the final work of the trip was done in the Uintah Mountains and on their southern slopes. Three weeks were spent here, and proved as profitable as any of the twelve that were spent in the field.

A large amount of material was secured, and among the several hundred species are many of great interest, either because of their meager representation in the herbaria, or because they are poorly understood, or finally because they have heretofore wholly escaped recognition. A discussion of a few of these is submitted in this paper.

CENTROSTEGIA Gray, DC. Prod. **14**:27; Pacif. R. Rep. **7**:19.

C. CRYPTANTHA (Curran); *Chorizanthe Thurberi cryptantha* Curran, Bull. Cal. Acad. **1**: 275.

C. LEPTOCERAS Gray, Proc. Am. Acad. **8**: 192; *Chorizanthe leptoceras* Wats., Proc. Am. Acad. **12**: 269.

C. THURBERI Gray, DC. Prod. **14**: 27; Pacif. R. Rep. **12**: 19; *Chorizanthe Thurberi* Wats., Proc. Am. Acad. **12**: 269.

The validity of the genus Centrostegia can hardly be questioned when one has both plants and descriptions at hand. The spurs on the involucre are so characteristic that the genus might well stand on these alone.

Eriogonum revolutum, n. sp.—Perennial, the low woody base rather intricately branched, the upright branchlets 7–10^{cm} long: leaves thick, linear, so strongly revolute as to be nearly terete, obtuse or acutish, 8–15^{mm} long, softly pubescent above, more densely so below, short petioled, fascicled near the ends of the branchlets: peduncles 5–8^{cm} long, slender, pubescent, leafy at the base only: involucres pubescent, short peduncled, in a compact head, turbinate, strongly 5-nerved and toothed, 10–20-flowered: bracts linear, scarcely exceeding the involucres; pedicels 4–5^{mm} long: calyx pubescent, pink, campanulate, slightly constricted in the middle, outer lobes oblong-oval, inner slightly narrower.

This excellent species is apparently not closely related to any described species, but undoubtedly belongs in § 3 of Watson's revision, Proc. Am. Acad. **12**: 262.

Collected by the writer in the mountains south of Bunkerville, Nevada (no. 753).

Cerastium variabile, n. sp.—A perennial cespitose herb with many erect stems 15–25^{cm} long, viscid pubescent throughout: leaves subcoriaceous, exceedingly variable in shape and size; the lower ones oblong-clavate, obtuse, 1–1.5^{cm} long; upper ones from narrowly oblong-linear to ovate-lanceolate, mostly acute, one-fourth to one-half the length of the internodes: sterile shoots very few, with internodes usually exceeding the oblong-linear acute leaves: flowers 5–12, in an elongated open cyme; the lower pedicels much elongated (often 25^{cm} long); upper ones considerably shorter, erect or recurved: the thick sepals narrowly oblong, acutish, 6–7^{mm} long, narrowed abruptly into a thin scarious margin and tip: petals 1–2^{mm} longer than the calyx, narrowly obcordate except for being *deeply* two-cleft: capsule one and a half times as long as the calyx, distinctly curved.

This very variable plant is most closely related to Dr. Greene's *C. occidentale*, from which it is easily distinguished by its more compactly cespitose

bunches with very few sterile shoots, by its remarkably viscid pubescence, elongated cymes, broader and thicker calyx lobes, and much shorter and more deeply cleft petals.

Collected by the writer in the Uintah Mountains, Utah (no. 1246), where it grew in some profusion.

Draba valida, n. sp.—Perennial with a tap root: stem usually single but much branched from the base; stem and branches somewhat rigidly erect, the main stem 1.2–2 dm high, exceeding the branches by 4–5 cm; rather finely hirsute throughout: basal leaves numerous, 1.5–2 cm long, spatulate, obtuse, entire or coarsely toothed: stem leaves sessile, oblong, entire or occasionally coarsely two to four toothed, 1–1.5 cm long; calyx oblong, obtuse, 1.5–2 mm long, sparingly clothed externally with long hairs: petals white, oval to obcordate and attenuate at base, 2–3 mm long: pedicels erect, stout, 2–4 mm long: pods oblong, 4–7 mm long, clothed with short branched hairs: stigma almost sessile.

The type (no. 1402) of the above species was collected by the writer at Dyer Mines, Uintah Mountains, Utah.

AMELANCHIER RUBESCENS **cinerea,** n. var.—A peculiarly ashy-colored divaricate shrub, distinguishable from *A. rubescens* Greene by the much denser pubescence on the leaves and inflorescence, by the nearly obtuse oval leaves which are acutely serrate to the base, and by the shorter more broadly campanulate calyx with linear acute lobes.

Collected by the writer at St. George, Utah, May 13, 1902 (no. 780).

Cowania alba, n. sp.—A quite freely branched bush, 1.5–2.5 m high, with white bark and light colored wood: leaves 3–5-cleft at the ends and tapering to rather broad petioles, 8–11 mm long, dark green above, somewhat viscid and barely tomentose beneath, edges strongly revolute and resinous-dotted, crowded at the ends of small branchlets which are scaly from the persistent stipules of previous years: flowers white, about 15 mm in diameter: calyx tube very narrowly funnelform, clothed with short silvery pubescence, usually slightly resinous-dotted (not glandular-tipped pubescence), strongly veined; lobes narrowly oblong, obtuse, strongly net-veined, 3 mm long: petals oblong, obovate, very irregu-

lar in size and outline but usually long clawed: akenes normally two (rarely three), large, 8 mm long and 2 mm wide, with a prominent keel along the back; length of the tails unknown.

This elegant species cannot be said to be closely related to any other. The number and size of the akenes and the shape of the leaves are very characteristic.

Collected by the writer in the mountains south of Bunkerville, Nevada (no. 744).

Geranium longipes (Wats.).—Annual: stems usually simple below, branched above, one to several from the same root, sparingly strigose with short reflexed hairs; above, at the second or third whorl of leaves, the stem breaks up into three to six equal slender branches which in turn branch out into the two-flowered, much elongated, nearly filiform peduncles: pedicels slender and elongated; peduncles and pedicels quite densely glandular-pubescent: leaves broadly reniform in outline, 3–5 cm wide, deeply 5–7-cleft nearly to the base, the divisions narrowly lobed; radical leaves numerous, on slender petioles, 10–15 cm long: flowers white or pinkish, 2.5–3 cm in diameter: sepals narrowly oblong, ciliate, pubescent on the prominent veins, terminating in a long awn: petals a little shorter than the sepals, narrowly obcordate, deeply triangulate-notched: lobes of the ovary coarsely strigose-pubescent; filaments persistent, as long as the lobes of the ovary; beak 2 cm long, rather long-pointed: seeds oblong, pitted.

It is apparent from the meager description of *G. carolinianum longipes* Wats. that it must have been drawn from inadequate material. The "usually solitary peduncle" of Mr. Watson's description is true of occasional western plants, but these can by no means be separated from the other western forms. All the western material I have seen (except one specimen of true *G. carolinianum* from Idaho, which was doubtless an introduction) has the elongated peduncles and pedicels, and this has led me to think that all our western material comes under Dr. Watson's *G. carolinianum longipes*. The character of the pubescence as well as the elongated peduncles and pedicels, together with such minor points as the narrower calyx lobes, longer point on the beak, etc., easily separate the western plant from the eastern.

The writer's no. 1395 from the Uintah Mountains, Utah, is considered typical.

Rhus macrothyrsa, n. sp.—A tree-like shrub 1.5–2.5 m high, with glabrous stems (except the base of the young shoots which

are clothed with a thick, light brown, woolly pubescence): leaves 20–25^{cm} long; rachis terete or often angled, with a narrow dorsal canescent line; leaflets 9–15, glabrous and green above and below, oblong-lanceolate, acuminate, acutely serrate, sessile: fruiting thyrse 15–25^{cm} long, open and quite strongly recurved; the rachis and its branches clothed with a rather coarse persistent pubescence; its branches often 8^{cm} long, ascending, subtended in the young thyrse by linear bracts 5–20^{mm} long: drupe slightly laterally compressed, about 3^{mm} in diameter, clothed with short, light red pubescence: stone nearly globular and smooth.

R. macrothyrsa is most closely related to *R. glabra*, from which it can readily be distinguished by its dark green leaves which are not at all glaucous on either side, and its long open recurved thyrse.

Collected by the writer (no. 988) at Calientes, Nevada.

Rhus utahensis, n. sp.—Shrub 1–1.5^{m} high, diffuse, rather slender: leaves simple, suborbicular or subreniform, truncate at base, coarsely and somewhat evenly crenate, 1.3–2^{cm} long: petioles terete, minutely pubescent, 4–8^{mm} long: inflorescence few-flowered: drupes rather large, 5–8^{mm} in diameter, clothed with a short pubescence.

R. utahensis is apparently the *R. canadensis simplicifolia* Greene, which name is untenable, however, on account of *R. simplicifolia* Salisb. *R. utahensis* is well worthy of specific rank, as it is very distinct from *R. trilobata*, its nearest ally.

Collected by the writer (no. 832) in Diamond Valley, Utah.

Apocynum nevadense, n. sp.—Glabrous throughout, stem 1–1.5^{m} high, freely branched above, the paired lateral branches far surpassing the central stem: leaves very smooth, subglaucous below, slightly darker above: the cauline sessile, semiclasping at base, 5–12^{cm} long, 2.5–4.5^{cm} wide, perfectly oblong, decidedly obtuse but tipped with a minute cusp, cordate at base; the rameal elliptic, acute, strongly murcronate, tapering below to the short petiole: cymes 1–3, usually terminal on the main stem, occasionally on the branches: peduncles 1–3^{cm} long; pedicels subtended by linear acute bracts: calyx segments linear-lanceolate: corolla white, cylindrical, exceeding the calyx segments by one-half: fruit 9–11^{cm} long.

This plant is probably most closely related to *A. oblongum* Greene, but

the sessile cordate semiclasping base of the cauline leaves and long fruits are distinguishing characters of *A. nevadense*.

The type no. 986, was collected at Calientes, Nevada, by the writer, May 29, 1902.

Cressa depressa, n. sp.—A depressed, spreading, many-branched, very leafy perennial 10–15^{cm} high, usually much broader, widely divaricately branched from the base up and canescently villous throughout: leaves oblong, subacute at both ends, subpetiolate, 5–10^{mm} long, 3–4^{mm} wide: flowers pediceled (pedicel 2–4^{mm} long) in the axils of the leaves, forming long narrow racemes, the branches being floriferous nearly to the base: calyx composed of 4 or 5 equal, oblong to nearly oval sepals 5^{mm} long, subtended by two small (usually half the length of the sepals) foliar bracts: tube of the corolla campanulate, the length of the sepals; lobes 5, oblong, subacute, reflexed, clothed exteriorly with long silky pubescence: filaments scarcely exserted, broadly subulate, inserted on the middle of the corolla tube and united a little below the insertion by their expanded bases, forming nectariferous pits: styles filiform, nearly twice the length of the corolla tube; ovary broadly ovate, copiously silky-lanate at summit, four-ovuled.

C. depressa is most closely related to *C. truxillensis*. The latter apparently differs little from the foreign *C. cretica*, resembling it in habit and character of the inflorescense. The generic description and figure in Engler and Prantl's *Nat. Pflanz.* **4**: 15 show the spicate or even nearly capitate character of the inflorescence which forms a great contrast to the raceme of *C. depressa*. The generic description in Benth and Hook. *Gen. Pl.* **2**: 881 calls for the inflorescence as described by Engler and Prantl. The generic descriptions all show that the previously described species have filiform filaments, whereas *C. depressa* has remarkably dilated filaments.

Collected by the writer (no. 726) from the salt swamp along the Virgin River of southern Nevada.

Langloisia punctata (Coville).—*Navarretia setosissima punctata* Coville, Contrib. U. S. Nat. Herb. **4**: 154.

The distinctions between *L. punctata* and *L. setosissima* are well brought out by Dr. Coville, and in the light of his discussion, in connection with good specimens of *L. punctata* recently collected by the writer at Rioville, Nevada, it seems proper to raise it to specific rank.

Phacelia foetida, n. sp.—Densely glandular-hispid throughout,

light olive-green, 4–6^{dm} high, stout, erect, from a biennial root: leaves oblong, deeply toothed and occasionally slightly lobed; the lowermost short-petioled, 5–8^{cm} long, densely tufted about the base; the upper sessile and numerous along the stem: inflorescence a dense spicate thyrsus 1–2^{dm} long, composed of short dense scorpioid cymes (occasionally compound cymes at base): flowers sessile: sepals clavate, 4–5^{mm} long: corolla white or cream colored, narrowly campanulate, 5–7^{mm} long, slightly hispid without, the lobes short (1^{mm} long), ovate, obtuse: anthers ovate-oblong; filaments slender, exserted half their length, inserted low down in the corolla tube; appendages ovate, obtuse, united at the base of the filaments: style 2-cleft two-thirds its length: capsule globose, slightly 4-lobed, short glandular-pubescent, 4-seeded.

The above species seems sufficiently distinct from all other species of Phacelia to require no explanatory notes. It grows in the lava fields of southern Utah, where it was collected by the writer. It is characterized by a deathly sickening odor which may account for the fact that apparently it has not been collected or described before.

PHACELIA PALMERI Torr., Watson, Bot. King 251.—*P. integrifolia Palmeri* Gray, Syn. Fl. **2**: 160.

From a recent collection, made by the writer, at Kernan, Nevada, of *P. Palmeri*, it seems proper that the plant should stand as a species. *P. integrifolia* has entire crenately-toothed leaves, whereas *P. Palmeri* is deeply sinuately lobed and the lobes sinuately toothed. The former also has long exserted stamens, while the stamens of the latter are shorter than the corolla. There is also a marked difference in the internal appendages of the two species.

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BRIEFER ARTICLES.

SELECTED NOTES. III.

(WITH SEVENTEEN FIGURES)

EQUISETUM ARVENSE L.—Though Hofmeister[1] has described in detail the sprouting spores of *Equisetum limosum* and *E. arvense*, his figures of the latter are not so full but that another series might be of interest; especially as the method of development varies so greatly in this species. I have followed carefully the young prothallia of *E. arvense* during a month of growth, and the figures here given illustrate their progress from day to day. In both *E. limosum* and *E. arvense*, Hofmeister finds that almost without exception there is first cut off in the germinating spore a comparatively colorless basal cell, which generally gives rise to the first rhizoid. In *E. arvense*, however, he finds that there are numerous exceptions to this, the small basal cell often not elongating into a rhizoid, but remaining unchanged, while the large cell above produces the rhizoid. This variation was very rare in the spores sprouted by me, but such a case is shown in *fig. 8*. Sometimes (*fig. 6*) the small cell was not cut off, but the rhizoid came directly from the base of the large cell. The first rhizoid is usually the only one for a long time, and in no case did I find another, even in the oldest stages figured. The second wall is as a rule nearly parallel to the first in *E. arvense*, while in *E. limosum*, according to Hofmeister, it is generally perpendicular or strongly inclined to it.

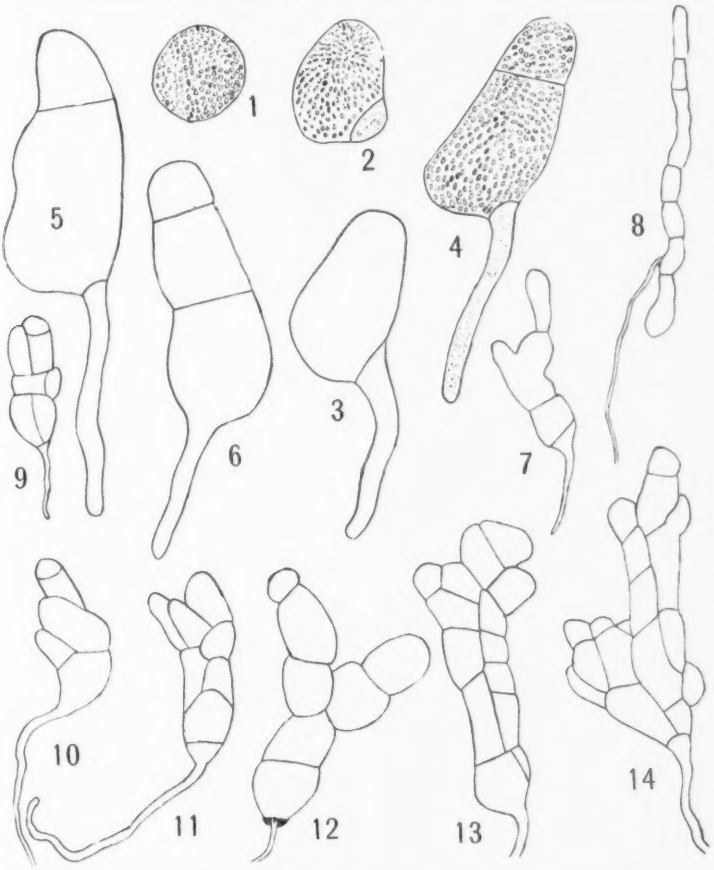
Comparing *figs. 8* and *9*, it will be seen that the greatest possible variation is met with. Both plants shown are of the same age, twenty-three days. The filamentous form (*fig. 8*) is very rare, and is not described by Hofmeister. But Campbell[2] finds that in *E. telmateia* "the first wall may be either vertical or transverse, and sometimes, but not often, there are several transverse walls, and a short filament is formed."[3] *Figs. 10–14* represent plants about one month old. The largest is about old enough to produce antheridia. Later stages were not followed.

[1] Vergleichende Untersuchungen der höherer Kryptogamen, Leipzig. 1851.

[2] Mosses and Ferns 424.

[3] I have not been able to see the papers of Sadebeck and Buchtien on Equisetum.

MULTISEEDED ACORNS. — Acorns with more than one seed have been described before, but the following striking example may not be unworthy of mention. On the bank of a stream near Baltimore, Md., there is a rock chestnut oak (*Quercus Prinus* L.) that was found to bear



FIGS. 1–14.—Different stages of sprouting spores of *Equisetum arvense*.

acorns which almost invariably contained two or three seeds. One of these acorns is shown sprouting in *fig. 15*. All three young plants are strong and healthy, but one is slightly larger than the others. I have found two young plants coming from an acorn of *Quercus velu-*

tina Lam., but other acorns from the same tree showed no such tendency.

CLAVARIA MUCIDA Pers. —This pretty little species has an interesting habit that I have seen referred to only by Morgan,[4] who describes it as "usually growing on a thin greenish stratum, Chlorococcus." I have often found this plant, and it has always been associated with this alga.[5] It generally grows on dead, soggy wood, but often also on alga-covered soil. The habit is shown in *fig. 16*. Atkinson describes and gives a photograph of *C. mucida*,[6] but does not mention its association with the alga. Neither does Hennings in Engler& Prantl's *Pflanzenfamilien*, who says in reference to its habit, "Auf faulenden Holze, seltener auf Erde."

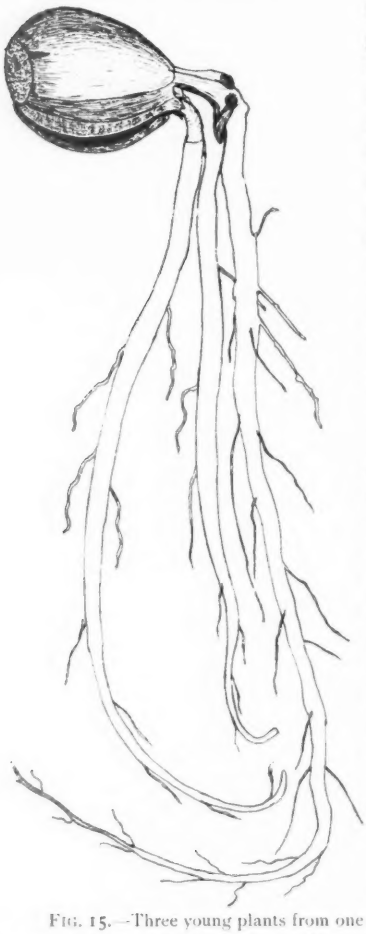


FIG. 15.—Three young plants from one acorn of *Quercus Prinus*. Natural size.

If the basal part of the fungus and the substratum be cut in paraffin or teased under the microscope, it will be seen that the delicate hyphae ramify from the base of the stalk and pass out in all directions among the alga cells. *Figure 17* illustrates the relation between alga and fungus. The hyphae do not enter the alga and have no haustoria, but show about the same loose relation with the alga as in the case of the lichen, Collema. From its constant occurrence and close association with this alga there seems scarcely a doubt that *Clavaria mucida* is in the initial stages of becoming a basidiomycetous lichen.

[4] The mycologic flora of the Miami Valley, Ohio. Jour. Cincinnati Soc. Nat. Hist. 11 : 86–95. *pl. 2*. 1888.

[5] I have not carefully identified the alga, and cannot vouch for its being Chlorococcus.

[6] Mushrooms, edible, poisonous, etc. Ithaca. 1900.

SPORE DISTRIBUTION IN LIVERWORTS.—It has no doubt been noticed by all observers of the liverworts that, while terrestrial species have as a rule (Riccia and Sphaerocarpus are exceptions) their capsules raised on elongated stalks furnished either by sporophyte or gametophyte, those which grow on trees seldom elongate their stalks more than enough to free the capsule from the perianth. This difference is plainly due to the fact that the arboricolous species are sufficiently elevated to allow their spores to be well scattered without any special contrivance. It is interesting to note, however, the behavior of the fertile branches of *Porella*

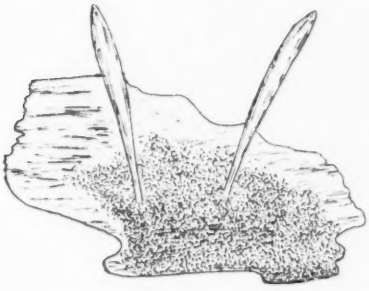


FIG. 16.—*Clavaria mucida*, growing on alga-covered wood. × 5.

FIG. 17.—*Clavaria mucida*. Hyphae surrounding groups of algae. Highly magnified.

platyphylla Lindb. While the vegetative branches of the liverwort remain closely appressed to the bark of the tree, the fertile shoots bend away some time before the spores are ripe, and often project a centimeter or more from the substratum. This exposes the spores to the free play of the wind and no doubt prevents many of them from being caught by the leaves of the mother plant. This habit seems to show that even in arboreal forms it may be an advantage to have the capsule removed some distance from the substratum. It will be noticed here that Porella resembles the Marchantiaceae in giving over to the gametophyte the duty of lifting the capsules.—W. C. COKER, *University of North Carolina, Chapel Hill.*

ON THE INTERPRETATION OF THE QUADRIPOLAR SPINDLE IN THE HEPATICAE.

SEVERAL papers have appeared recently bearing on the subject of the quadripolar spindle in the Hepaticae, particularly in connection with the genus Pellia. As the writers do not always seem to have

apprehended the views I put forward in 1895 respecting this structure, or the degree of importance I attached to it, I may perhaps be permitted to explain the position I then took up, especially as I have seen no reason seriously to depart from it since that time. The structure in question was first seen by me in *Pallavicinia decipiens*. In this form the deeply lobed character of the spore mother-cell is marked in the highest degree, and I afterwards found the same structure in other Jungermanniales in which the spore mother-cells present similar characters.

Now I expressly regarded the appearance of four centrospheres, whether I was able to distinguish centrosomes (Fossombronia) or not as bodies contained within them, as a phenomenon *to be correlated with the lobed character of the cell taken as a whole*. But I certainly did not regard its persistence throughout the first mitosis as an essential condition. It does not so persist in Fossombronia, or in any other forms but *Pallavicinia decipiens*, and far less regularly in Pellia.[7] In summing up the body of evidence, I said (*l. c.*, p. 510): "The quadripolar spindles of these Hepaticae are really only the result of the special conditions imposed by the configuration of the spore mother-cell."

It is clearly, therefore, a misleading rendering of my position, as adopted in 1895, to suggest that the quadrupling of the primary chromosomes and their simultaneous distribution into four groups to form the daughter-nuclei constitute the "most remarkable features of Farmer's account of the activities of the quadripolar spindle."[8]

From the first, as soon as I began to extend my observations made on *Pallavicinia decipiens* to other species of Hepaticae, I recognized that this formed a very special case, and I correlated it with the unusually deep lobing of the spore mother-cell. I do not myself at all regard the quadrupling of the chromosomes and their simultaneous distribution as the point of central interest. It is even possible that future investigation, with the help of more modern methods, may show that the two divisions were not so much compressed as I thought in 1894, and that a cell plate may after all be formed during the first mitosis.

I may say in passing that I am not surprised that the character of the mitosis in *P. Lyellii*, described by A. C. Moore, should differ from that in *P. decipiens*. He depicts a slightly four-lobed cell, somewhat recalling that of Fossombronia, or Aneura, and I am much interested to see that, as one would have anticipated, the general features of the karyokinesis resemble those presented by the species of the latter genera with which I am familiar. A. C. Moore is right in supposing that I should interpret his *fig. 1* as indicating a less pronounced stage of

[7] Annals of Botany **9**: 475. [8] MOORE, A. C., BOT. GAZ. **35**: 388. 1903.

what in *P. decipiens* becomes a very well marked four-rayed figure. I observe he does not figure centrosomes or centrospheres, such as are easily seen at the corresponding stage in Aneura or Fossombronia. I fancy these bodies are not always identically developed, perhaps even in closely related forms. I have become convinced that in many liverworts there are often present within the centrosphere, where it can be distinguished, one or more particles that may be looked on as representing a centrosome. The number is, I think, of no great moment. The existence of the *substance*, whether in one or more granules, is the essential point. A nucleolus does not cease to be a nucleolus because several of them may be present in a nucleus which more frequently only contains a single one, and the same argument applies, I think, to the centrosome substance where it can be identified at all.

And as to the quadripolar spindle, whether we choose to restrict the term "spindle" to that portion of the achromatic apparatus that has become continuous from pole to pole, or whether we prefer to extend it so as to include the fibers or substances that are differentiated between the centrospheres and the nucleus during the prophase, irrespective as to whether these retain their positions later or not, is a matter of individual taste. Personally, seeing that they form a stage in the differentiation of the interpolar spindle (with or without fusion in pairs or otherwise), I embrace the latter alternative; and so include the four-rayed figure, independently of its degree of development or permanence as part of the spindle apparatus. I do not think much is gained by limiting the term "spindle" to the later stages, or restricting it purely to bipolar forms.

I should like to take this opportunity of correcting a statement in the memoir on nuclear division to which I have already referred in this note. At the time that paper was written the terms "heterotype" and "homotype" had not acquired that definite meaning that now attaches to them. At the present time I should certainly not regard the second division of the spore mother-cell as in any case in essential characters being really of a heterotype nature. The small size of the objects makes an exact appreciation of their evolution and final form a matter of some difficulty. I have, however, no reason to suppose that those few instances in which a renewed examination of the question has not resulted in definitely settling their homotype character, do really in any way differ in this respect from the many forms in which the nature of the second mitosis can be satisfactorily ascertained.—J. B. FARMER, *London, England.*

CURRENT LITERATURE.

BOOK REVIEWS.

Evolution and adaptation.

UNDER THE ABOVE TITLE the author has published a critical examination of the current ideas regarding the origin of adaptations.[1] His extended work on regeneration showed very plainly the insufficiency of the natural-selection theory as an explanation of the phenomena of that field. The present work is an extension of the same idea to the whole biological field, as the result of a study of the general problem from the same point of view. The appearance of De Vries's *Mutationstheorie*, and the republication of Mendel's experiments in heredity, with the correlated work of the last three years, have greatly strengthened the stand which the author is able to make; for antagonism is shown towards the principle of selection only in so far as it claims to be an active agent in the origin of adaptations. While there may be some doubt, especially in his later writings, as to the extent to which Darwin really meant to imply that the selective agent involved in the survival of adaptations is also directly involved in their origin, it is certain that the idea of the activity of natural selection in the *production* of adaptations has been carried to an absurd extreme by some of Darwin's followers. It is especially against this extreme position that the author takes a stand, for the usefulness or non-usefulness of a structure can have nothing to do with its origin. The selective factor, however, may be of value on one side of the problem of adaptation, "for," to use the author's words, "while we can profitably reject much of the theory of natural selection, and more especially the idea that adaptations have arisen because of their usefulness, yet the fact that living things must be adapted more or less well to their environment in order to remain in existence, may after all account for the widespread *occurrence* of adaptation in animals and plants."

This statement gives the prevailing point of view throughout the book, though the book is by no means merely a development of the above idea. It is especially marked by its judicious treatment of the different phases of the question, and by its careful exposition of opposing views. As examples may be mentioned the exposition of Nägeli's view of a perfecting principle throughout organic nature and of Fleischmann's criticism of the theory of evolution. The numerous original ideas may be represented by the following example chosen at random. In the discussion of the recapitulation theory the author gives the details of his interesting theory of embryonic repetition,

[1] MORGAN, T. H., Evolution and adaptation. 8vo. pp. xiii+470. New York: Macmillan Co. 1903.

in which he holds that we cannot compare an embryonic characteristic with an *adult* ancestral one, but that embryonic characters only can be compared. "Their resemblances are explained on the assumption that there has been an ancestral adult form having these embryonic stages in its development, and these stages have been handed down to the divergent lines of its descendants."

The wide scope of the work may be indicated best by an enumeration of the titles of the different chapters. There is a chapter on the problem of adaptation, two on the theory of evolution, three are devoted to a criticism of the theories of natural selection and sexual selection, then come successively, the inheritance of acquired characters, continuous and discontinuous variation and heredity, evolution as the result of external and internal factors, the origin of the different kinds of adaptations, tropisms and instincts as adaptations, sex as an adaptation, and finally a summary with general conclusions.

The book is a valuable one both for its clear statement of the problems under discussion and for its many new ideas. It will undoubtedly be read by a wide circle of biologists and others interested in questions of evolution and adaptation.—CHARLES ZELENY.

The cell of the Cyanophyceae.

IN REGARD to the structure of the cell of the Cyanophyceae, observations, interpretations, and theories have long been conflicting and often contradictory, some observers describing a nucleus and chromatophores, and others denying the existence of such structures, while only less difference of opinion has been manifested in regard to other cell contents, the membranes, gelatinous envelopes, and the heterocysts. Kohl has just published a book[2] in which he first gives a critical discussion of previous literature, paying particular attention to the work of Bütschli, Hegler, Palla, Fischer, Zacharias, and Brand. He then describes his own work in great detail, with full illustrations on ten colored lithograph plates. Tolypothrix, Nostoc, and Anabaena are the principal forms studied and nearly all of the figures are from *Tolypothrix lanata* and *Nostoc coeruleum*.

The following topics are treated: central granules, cyanophycin granules, oil, chromatophores, glycogen, membrane and partitions, protoplasmic connections, "Verschlusskörper," vacuoles, chromatic substance, heterocysts, concave cells, central body; with some remarks on the relationship between the Cyanophyceae and bacteria. There is also a valuable table containing the most important tests and staining reactions. Without attempting to separate original views from confirmations and contradictions, the author's results, as gathered from the summary and body of the work, are about as

[2] KOHL, F. G., Ueber die Organization und die Physiologie der Cyanophyceenzelle und die mitotische Teilung ihres Kernes. 8vo. pp. 240. *pls.* 10. Gustav Fischer, Jena, 1903. *M* 20.

follows. The protoplast of the Cyanophyceae does not differ essentially from that of other plant cells, having a nucleus and peripheral cytoplasm with chromatophores. There is always a single nucleus, organized as an independent organ and consisting of a relatively faintly staining ground mass in which the chromatin is imbedded and a larger or smaller number of "central granules" which are not found outside the nucleus. The nucleus differs from that of the higher plants (1) in the absence of a nuclear membrane,[3] (2) in the absence of nucleoli, and (3) in its form. The cytoplasm contains chromatophores, oil drops, cyanophycin granules, glycogen, and vacuoles. The chromatophores contain chlorophyll, carotin, and phycocyanin. The product of assimilation is glycogen, starch not being demonstrable, and the cyanophycin granules represent reserved albumen. The membranes of the vegetative cells are not cuticularized but consist principally of chitin, while those of the heterocyst are mostly cellulose. There are innumerable small chromatophores. The oft discussed central body is a genuine nucleus. During mitosis a spirem is formed which breaks up into chromosomes, and the various phases bear so striking a resemblance to those of higher plants that the author does not hesitate to designate them as *spirem*, *equatorial plate*, *diaster*, and *dispirem*. Threads resembling a spindle are shown in several figures. Protoplasmic connections between vegetative cells have been demonstrated in many cases. Chromatin is said to be a constant constituent of the cells of the bacteria as well of those of the Cyanophyceae, and Kohl believes that the two groups are very intimately related.—C. J. CHAMBERLAIN.

Handbook of systematic botany.

THE SECOND PART of Wettstein's handbook,[4] which has just appeared, deals with bryophytes, pteridophytes, and gymnosperms; the remaining section, which is to treat of angiosperms, will contain the index and will complete the work. The author proposes a complete system of classification, the main features of which were given in the review of the first part.[5] The taxonomic characters of the larger groups, of families, and sometimes of the most important genera, are given and the classification determines the order of treatment. However, the book is of equal interest to the morphologist, for development and embryology are carefully treated and are constantly used to support the author's views of relationships. The illustrations representing the development of organs from the standpoint of comparative morphology are particularly instructive, as is also the plate illustrating the evolution of plants, from the algae to the angiosperms. Considering the able

[3] No reference is made to the work of Lawson, who, in the BOTANICAL GAZETTE for May 1903, discussed the absence of the nuclear membrane in the Cyanophyceae.

[4] WETTSTEIN, R. v., Handbuch der systematischen Botanik. II. Band, Theil I. 8vo. pp. 160. 1 colored plate, figs. 100. Leipzig and Wien: Franz Deuticke. 1903. *M* 4.

[5] BOT. GAZ. **32**: 61–62. 1901.

manner in which the morphological part of the work is treated, one is hardly prepared for the statement that in gymnosperms there is no alternation of generations, although traces of alternation are demonstrable, while in angiosperms the reduction of the prothallium has proceeded so far that sure homologies can no longer be shown and the alternation of generations has entirely disappeared. Of particular interest are the introductory pages on the evolutionary composition of groups, the homologies between them, and the causes of the changes in the homologous organs of the cormophytes.

The bryophytes are subdivided, as usual, into Musci and Hepaticae; in the pteridophytes three groups are recognized, the Filicinae, Equisetinae, and Lycopodinae; the gymnosperms are subdivided into six classes, Cycadinae, Bennettitinae, Cordaitieae, Ginkgoanae, Coniferae, and Gnetinae.—C. J. CHAMBERLAIN.

NOTES FOR STUDENTS.

RENAULT[6] concludes from the study of a number of plant sections that vegetative activity was greater in the Carboniferous age than at present. An extraordinary development of vascular and other tissues is recounted and figured.—H. C. COWLES.

ARBER[7] has recorded *Glossopteris Browniana* Brongn. from Sisi in Rhodesia, the containing formation being probably Permo-Carboniferous. A species of Calamites is recorded from the Tuli coalfield; and the Sengwe coalfield in northern Matabeleland yields an undetermined specimen of wood and two stems of the Eu-Sigillarian Rhytidolepis type.—E. W. BERRY.

MOLLIARD finds[8] that in pure cultures of *Ascobolus sp.* perithecia are not developed, although there is a considerable development of the vegetative mycelium. In all cases of fruiting individuals bacteria are present in abundance. He thinks that this is a fact of large significance, though he has no suggestion as to the exact office of the bacteria in this interesting case of symbiosis.—H. C. COWLES.

SEWARD[9] describes a new species of Dictyozamites from a low horizon in the Estuarine series of the Inferior Oolite of Yorkshire. The genus and its distribution in Jurassic times are discussed somewhat fully, and a comparison is instituted between the lower Mesozoic floras of Japan, Bornholm,

[6] RENAULT, B., Sur l'activité végétative aux époques anciennes. Compt. Rend. **136**: 401–403. 1903.

[7] ARBER, E. A. N., Notes on some fossil plants collected by Mr. Molyneux in Rhodesia. Quart. Jour. Geol. Soc. Lond. **59**: 288–290. 1903.

[8] MOLLIARD, Rôle des bactéries dans la production des périthèces des Ascobolus. Compt. Rend. **136**: 899–901. 1903.

[9] SEWARD, A. C., On the occurrence of Dictyozamites in England, with remarks on European and eastern Mesozoic floras. Quart. Jour. Geol. Soc. Lond. **59**: 217–232. *pl. 15.* 1903.

India, and England, with the result that they show only minor differences facts contrary to the usually accepted view. The paper, which is an important one, concludes with a complete bibliography.—E. W. BERRY.

R. G. LEAVITT[10] has accumulated some interesting data in reference to what he calls reversionary stages in *Drosera intermedia*, stages that he has experimentally induced. These data support the general statement "(1) that reversions, in either an ascending or a descending direction, are sometimes occasioned in plants by a deficiency of the food materials supplied to developing parts; and (2) that reversions in either direction are sometimes occasioned by a superabundant food supply in developing parts."—J. M. C.

BALL[11] has recently reinvestigated the influence of strains upon the formation of mechanical tissue. His results do not agree with those of Hegler on the same subject, for by a gradual increase in the pull exerted upon young stems Ball was able to produce neither an increase in the ability to resist mechanical pulling nor any thickening of the tissues. He substantiates the results obtained by Wortmann and by Elfving that when a stem is inhibited by force from bending geotropically there arises a marked one-sided development of bast fibers and collenchyma on the upper side; and also when an organ is prevented by force from bending phototropically there is a notable increase in the tissues on the side toward which it would bend. An increased thickening was also obtained on the convex side of stems bent over mechanically with gravity neutralized by the clinostat.—W. B. MACCALLUM.

THE DEHISCENCE of sporangia[12] of gymnosperms is definitely related to their form and position, and favors the distribution of the spores. The nearly related Picea and Abies differ in the dehiscence of their sporangia, the dehiscence in Picea being longitudinal while in Abies it is transverse. The upright staminate strobilus of Picea requires a longitudinal dehiscence for a thorough discharge of the pollen, while a transverse dehiscence is more effective in discharging pollen from the drooping strobilus of Abies. The peculiar dehiscence in Taxus is adapted to a rapid discharge of the pollen. In Ginkgo the lines of dehiscence of the two sporangia face each other and lie at such an angle that the pollen is easily shed. Ginkgo is the only known gymnosperm which has an endothecium. The Cupressineae are not considered, because their small, rather spherical sporangia are not so definitely oriented as in the other groups.—C. J. CHAMBERLAIN.

NOEL BERNARD has added further data[13] in the line of his interesting

[10] LEAVITT, R. G., Reversionary stages in *Drosera intermedia*. Rhodora **5**: 265–272. 1903.

[11] BALL, O. M., Der Einfluss von Zug auf die Ausbildung von Festigungsgewebe. Jahrb. Wiss. Bot. **39**: 305–341. *pls. 6–7.* 1903.

[12] GOEBEL, K., Morphologische und biologische Bemerkungen: 13. Ueber die Pollenentleerung bei einigen Gymnospermen. Flora **91**: 237–263. *figs. 19.* 1902.

[13] BERNARD, NOEL, Conditions physiques de la tubérisation chez les végétaux. Compt. Rend. **135**: 706–708. 1902.

tuberization studies.[14] E. Laurent had shown that buds from aerial stems of the potato may develop into tubers, when placed in a sufficiently concentrated solution of saccharose, even when the latter is thoroughly sterilized; which seemed to call in question Bernard's theory that tuberization is due to an infection by parasitic fungi. Bernard confirms Laurent's results and extends them considerably, showing that a number of solutions produce like results. In these cases the chemical nature of the solution is shown to be of but little moment as compared with osmotic pressure. Bernard therefore enlarges his theory as follows: the state of hypertrophy which we call tuberization may be induced by various agents, which bring the cells into contact with substances of relatively high osmotic pressure. Among these substances in nature the products of fungus activity are perhaps the most important.—H. C. COWLES.

IN HIS second paper on the solenostelic ferns Gwynne-Vaughan [15] extends his observations to a large number of genera which he treats in a comparative way. His studies have led him to abandon Van Tieghem's term polystelic, for he finds that the meristeles are in all cases segments of a vascular ring, the lacunae in which are caused by the exit of leaf traces. The term solenostelic is applied to those cases where the foliar lacunae do not overlap, and this condition is derived from one in which the stele is solid. Evidence is adduced to show that the intrastelar parenchyma is merely cortex which has intruded through the leaf-gaps. Thus Gwynne-Vaughan's view of the fern stele coincides with that already advanced by Jeffrey, although rather strangely no mention is made of this fact, and is opposed to that of many English writers. The internal vascular strands found in Cyatheaceae are considered to be derived from elaboration of a local thickening of the xylem ring at the margin of the leaf gaps. The present system of classification is considered to receive support from the anatomical data presented, since nearly all the genera regarded as primitive by Prantl have a primitive vascular structure.—M. A. CHRYSLER.

THE SPERMATOGENESIS of hybrid peas [16] appears as the second paper in Dr. Cannon's studies in plant hybrids. Two hybrid peas were used for the present investigation, one a hybrid between the pure races Fillbasket and Debarbieux, and the other between Express and Serpette. Both hybrids are fertile and show variation according to the law of Mendel. Spermatogenesis was studied both in the pure races and in the hybrids. In the cells of the gametophyte the number of chromosomes is seven in all the pure forms and

[14] See BOT. GAZ. **33**: 75. 1902.

[15] GWYNNE-VAUGHAN, D. T., Observations on the anatomy of solenostelic ferns. II. Ann. Botany **17**: 690–742. 1903.

[16] CANNON, W. A., Studies in plant hybrids: the spermatogenesis of hybrid peas. Bull. Torr. Bot. Club **30**: 519–543. *pls. 17–19*. 1903. For review of the first paper see BOT. GAZ. **35**: 445. 1903.

also in both hybrids. The number of chromosomes in the sporophytes of all the forms is fourteen. In the sporogenous division immediately preceding the formation of the mother-cells in both hybrids and in the pure form Fill-basket, the chromosomes were associated in pairs which may be related to the chromatin rings of the succeeding heterotypic division. Spermatogenesis in the hybrids proceeds just as in the pure races, and no abnormal mitoses were observed; consequently, abnormalities and irregularities of nuclear divisions do not form the basis for the variations of these hybrids. It is suggested that a thorough study of the sporogenous divisions preceding the heterotypic division may afford some explanation of variation.—C. J. CHAMBERLAIN.

AN INTERESTING account of the reproductive processes in Araiospora is presented by King.[17] Zoospores are formed through cleavage with the aid of vacuoles, and the outer plasma membrane is the last connecting film ruptured. The oogonium contains from 35 to 55 nuclei, which pass to the periphery simultaneously with the formation and fusion of patches of fine meshed cytoplasm in the center of the ooplasm. There is probably a general mitosis before the periplasm is differentiated from the ooplasm. A receptive papilla from the ooplasm pierces the antheridium and establishes the canal for the entrance of the sperm nucleus. There is no antheridial tube, the wall of the canal being of oogonial origin. This is a very interesting point, in which Araiospora appears to differ from all other oosporic Phycomycetes. The periplasm divides by anticlinal walls into hexagonal cells which invest the egg. The egg is uninucleate and a single sperm nucleus enters the ooplasm. These gamete nuclei approach in the central region of denser ooplasm and extend toward one another, later rounding off and lying side by side. They were not observed in process of fusion and this event, if it occurs, must be greatly delayed, for the pair may be found in the oldest oospores. The development and structure of the sexual organs indicates a closer relationship of Araiospora to the Peronsporales than to the Saprolegniales.—B. M. DAVIS.

THE REDUCTION of chromosomes, development of the embryo sac, and fertilization in *Paris quadrifolia* and *Trillium grandiflorum* have been investigated by Ernst.[18] The number of chromosomes in Paris is 24 in the sporophyte and 12 in the gametophytes, while in Trillium the numbers are 12 and 6 respectively. Since the two genera are so closely related, it is suggested that the double number of chromosomes in Paris may be due to an extra splitting of the chromatin thread. At the equatorial plate stage of the heterotypic division a second longitudinal splitting of the chromosomes is already

[17] KING, C. A., Observations on the cytology of *Araiospora pulchra* Thaxter. Proc. Boston Soc. Nat. Hist. **31**: 211. 1903.

[18] ERNST, A., Chromosomenreduction, Entwickelung des Embryosackes und Befruchtung bei *Paris quadrifolia* L. und *Trillium grandiflorum* Salisb. Flora **91**: 1–46. *pls. 1–6.* 1902.

evident, so that there can be no reduction division in Weissmann's sense. The statement that Trillium (with Naias) has the smallest number of chromosomes yet known in phanerogams reveals another oversight of American literature,[19] since the numbers in Canna are 6 in sporophyte and 3 in the gametophyte. In a few cases the embryo sac of Trillium showed ten nuclei instead of eight, the two extra nuclei having arisen through fragmentation of two of the eight nuclei.

Double fertilization occurs in both genera. In the union of the sperm nucleus with that of the egg, the fusion is complete, a resting nucleus being formed. The second sperm nucleus and also the two polar nuclei pass into the spirem condition before uniting, so that there can be no real fusion of chromatin in the formation of the endosperm nucleus. How long the chromatin of these three nuclei remains independent was not determined.—C. J. CHAMBERLAIN.

ALL ECOLOGISTS are acquainted with Bonnier's great contributions to experimental anatomy, especially in his studies of alpine plants. He has recently[20] presented a second communication dealing with his Mediterranean cultures, which were established near Toulon in 1898. Fifty perennial species were selected, each plant being split in two, so that cultures of the same individual were conducted at Toulon and Fontainebleau. The plants used were obtained at Fontainebleau, while the soil for the parallel cultures was taken from Toulon. The external characters of the Toulon individuals were noted in the first communication;[21] these characters have been only accentuated in the succeeding seasons, and the experimental plants have become quite like plants of the same species native about Toulon. The early secondary wood at Toulon contains vessels of larger caliber than at Paris, while on the other hand the later wood is more fibrous at the former place. Again, in autumn the Toulon wood contains vessels of large caliber. Bonnier thinks that the large early and late vessels at Toulon are to be correlated with the two rainy periods, while the fibrous wood of summer is correlated with a dry period. Paris, on the other hand, has a more uniform climate, which is moister in summer than that of Toulon. The annual ring is thicker at Toulon. Many differences in leaf structure are also noted; for the most part the Toulon leaf characters are the more xerophytic. The immense importance of this type of study is obvious; it escapes on the one hand the errors arising from hasty field generalizations, and on the other hand it is free from the untenable inferences often drawn from experimental

[19] BOT. GAZ. **30**: 25–47. *pls.* 6–7. 1900. See review in Jour. Appl. Micros. **3**: 1064–1065. 1900.

[20] BONNIER, GASTON, Cultures expérimentales dans la région méditerranéenne pour le modifications de la structure anatomique. Compt. Rend. **135**: 1285–1289. 1902.

[21] Compt. Rend. **129**: 1207–1213. 1899.

work conducted wholly in the artificial conditions of the laboratory or greenhouse.—H. C. COWLES.

IKENO has published his full account of spermatogenesis in *Marchantia polymorpha*,[22] following his preliminary announcement in the *Comptes Rendus*. He finds a centrosome beside each nucleus previous to the mitoses in the spermatogenous tissue. The centrosome divides, and its products, passing to opposite sides of the nucleus, become the poles of the spindle. He gives evidence that the daughter centrosomes sometimes divide again when at the poles of the spindle in anaphase. The centrosome cannot be found at the side of the daughter nucleus after the mitosis is completed, but it appears when the nucleus is ready for the next division. Ikeno believes that the centrosome is formed within the interior of each nucleus as a deeply staining body among the linin threads. This body moves to the nuclear membrane and is thrust from the nucleus. Outside of the nucleus it becomes the centrosome, functioning in the mitosis as described above. This account of the intranuclear origin of a centrosome is extraordinary. Intranuclear centrosomes have been reported in several animal forms, but they do not leave the nucleus in the manner described by Ikeno.

After the final mitoses in the spermatogenous tissue the centrosomes remain, to become the blepharoplasts of the sperms. Each blepharoplast passes to the plasma membrane of its sperm cell and develops two cilia. There is formed at this time another deeply staining body in the cytoplasm considered by Ikeno a *Nebenkörper*. The nucleus begins to elongate, this accessory body takes a position between it and the blepharoplast, and in this manner the much attenuated sperm is organized from the mother-cell.

Ikeno reasserts the blepharoplast to be the homologue of a centrosome, a position which he and Hirasé held in Cycas and Ginkgo respectively. In this they have the support of Belajeff's studies on Marsilia. Of an opposite view are Webber, Strasburger, and Shaw, who hold that there is no genetic relationship between the blepharoplast and the centrosome. The opinions of these authors cannot be discussed in a brief review, but the problem rests on disputed questions of fact as to the origin and behavior of blepharoplasts in all of the great groups of plants, from the processes of zoospore formation to the complications of spermatogenesis in the gymnosperms. There is no agreement on the events in any one type; which is eloquent of the desirability of cell studies of this character.—B. M. DAVIS.

ITEMS OF TAXONOMIC INTEREST are as follows: THEO. HOLM (Am. Jour. Sci. IV. **16**: 369–376. 1903), has made a morphological and anatomical study of *Hypericum virginicum*, often called Elodea, and has reached the conclusion that it represents the obscure but valid genus Triadenum of Rafinesque. Accordingly he writes the name *Triadenum virginicum* (L.) Raf.—THEO.

[22] IKENO, S., Die Spermatogenése von *Marchantia polymorpha*. Beihefte Bot. Centralbl. **15**: 65–88. *pl. 1*. 1903.

HOLM (*idem* 445–464), in his 20th "Studies in the Cyperaceae" has presented a natural classification of *Vigneae* and *Carices genuinae*, illustrating it by numerous species from various parts of the world which have been studied by the author, and were represented by sufficient material. In the *Vigneae* 15 sections are named, all excepting one being new; and in the *Carices genuinae* 24 sections are recognized, 11 of which are new. The classification follows the principles suggested by Drejer.—A. A. EATON (Fern Bull. **12**: 108–114. 1903) has described three new varieties of *Equisetum hiemale*.—H. DE BOISSIEU (Bull. Herb. Boiss. II. **3**:837–856. 1903), in a paper presenting the Umbelliferae of China, describes *Nelopterygium* (Symrnieae) as a new genus with two species, and also new species under Pimpinella, Seseli, Ligusticum, Selinum, Pleurospermum, Angelica, Peucedanum, and Heracleum.—M. L. FERNALD (Rhodora **5**: 247–251. 1903) has described a new Kobresia from Maine.—A. A. EATON (*idem* 277–280) has described three new varieties of Isoetes from Massachusetts.—R. MAIRE and P. A. SACCARDO (Ann. Mycologici **1**:417–419. 1903) have described a new genus (*Didymascella*) of Phacidiaceae.—GEO. V. NASH (Torreya **3**: 101–102. 1903) has described a new Aletris from Florida.—G. N. BEST (Bull. Torr. Bot. Club **30**: 463–482. *pls. 15–16*. 1903) has published a revision of the North American species of Leskea, recognizing 15 species and varieties, four of which are new.—MARCUS E. JONES (Contrib. Western Bot. 11) has described a new species of Leucothoe, has discussed western Nyctaginaceae, describing a number of new species under Eriogonum, and has presented his views concerning several western Chenopodiaceae, describing new species under Atriplex.—ALICE EASTWOOD (Bull. Torr. Bot. Club **30**: 483–502. 1903), in a paper entitled "New species of western plants," has described new species under Zygadenus, Allium, Fritillaria, Iris, Chorizanthe, Spraguea, Silene, Eschscholtzia (2), Arabis, Cleomella, Wislizenia, Lathyrus, Clarkia, Scutellaria (3), Fraxinus, Convolvulus, Sphacele, Monardella, Lappula, Symphoricarpos (4), Echinocystis, Nemacladus, Agoseris, and Crepis.—O. VON SEEMEN (*idem* 634–636) has described three new species of Salix from California and Nevada.—J. M. C.

RECENT CONTRIBUTIONS CONCERNING MYCORHIZA. Fungi have long been associated with certain liverworts, but NĚMEC[23] was among the first to make a careful study of the subject; it was his belief that they characterize the Jungermanniaceae rather generally, but that they are rare or absent in the Marchantiaceae. STAHL,[24] supposing this distinction to be true, applied his mycorhiza theory to the liverworts, considering the Jungermanniaceae to have weak transpiration, abundance of sugar, and mycorhiza, while the Marchantiaceae have strong transpiration, abundance of starch, and no mycorhiza.

[23] Ber. Deutsch. Bot. Gessells. **17**: 311–317. 1899.

[24] Jahrb. Wiss. Bot. **34**: 539–668. 1900. See BOT. GAZ. **30**: 68. 1900.

GOLENKIN, however, finds[25] that several of the Marchantiaceae, such as Marchantia, Preissia, Fegatella, have typical mycorhiza, although many species appear to be autotrophic. The fungus cells are localized, and in some cases are red in color. Starch is much more abundant in the cells that are free from fungi. BEAUVERIE[26] has made an experimental study of the mycorhiza of *Fegatella conica*, which he thinks to be of benefit to the host. Cultures in which the fungus (a Fusarium) occurs are more luxuriant than sterile cultures. Photosynthesis is weak, and the fungus is believed to obtain some of the necessary carbon. CAVERS[27] has made yet further studies of liverwort mycorhiza, but he adds little to our knowledge.

MÖLLER has been studying[28] the mycorhiza of pine roots, and obtains some results which differ from those of Frank. The well known ectotropic mycorhiza develops in connection with the roots of *Pinus sylvestris* in sand but not in humus, whereas Frank supposed the reverse to be the case. Where the fungus occurs, many of the roots, especially the main roots, are free from it; these roots are abundantly provided with hairs, which presumably have an absorptive function. Pines without mycorhiza are said to thrive quite well in humus soils. In raw humus soils a hitherto undescribed endotropic mycorhiza is found. Möller doubts if we yet know the physiological significance of mycorhiza; especially does he doubt whether it is proven that root fungi increase the supply of available nitrogen. TUBEUF,[29] on the other hand, though differing from Stahl, adheres in general to the prevalent mycorhiza theory. He thinks the chief value of the fungus to the host is in making nitrogen more available; atmospheric nitrogen in endotropic forms, humus nitrogen in ectotropic. Seven types of mycotrophic plants are recognized: (1) plants with occasional, and presumably non-essential, endotropic mycorhiza; (2) plants with strong endotropic mycorhiza, and with fully developed photosynthesis, transpiration, and absorption; (3) as in 2, except that the above-named functions are poorly developed (as Neottia), hence the fungi are probably of more consequence; (4) plants with occasional, and presumably non-essential ectotropic mycorhiza; (5) plants (as Pinus) with abundance of ectotropic mycorhiza and also of root hairs; (6) plants (Mono-

[25] GOLENKIN, M., Die Mycorhiza-ähnlichen Bildungen der Marchantiaceen. Flora **90**: 209–220. 1902.

[26] BEAUVERIE, J., Étude d'une hépatique a thalle habité par un champignon filamenteux. Compt. Rend. **134**: 616–618. 1902.

[27] CAVERS, F., On saprophytism and mycorhiza in Hepaticae. The New Phytologist **2**: 30–35. 1903.

[28] MÖLLER, A., Ueber die Wurzelbildung der ein- und zweijährigen Kiefer im märkischen Sandboden. Zeits. Forst- und Jagdwesen 1902–1903 (Bot. Centralbl. **89**: 583, **93**: 257; Bot. Zeit. **61**: 329).

[29] TUBEUF, C. VON, Beiträge zur Mycorhizafrage. Naturw. Zeits. Land- und Forstwirthschaft **1**: 67 ff., 284 ff., 1903 (Bot. Cent. **93**: 430, 520).

tropa) with ectotropic mycorhiza and no root hairs, all food-stuffs being supplied by the fungus; (7) plants with ectotropic and endotropic mycorhiza. Tubeuf discounts some of Möller's work by showing that *Pinus sylvestris* has luxuriant ectotropic mycorhiza in moors; *P. cembra* has similar root fungi in alpine humus.

Cytological mycorhiza studies have been made by SHIBATA[30] and HILTNER.[31] Shibata has confirmed the general results of W. MAGNUS,[32] and has gone into greater detail along similar lines. The infested cells of Podocarpus show enlarged and amoeboid nuclei, which divide amitotically; upon the death or resorption of the fungus ordinary mitosis occurs again, though without normal spindles and nuclear plates, the nucleus, too, soon disorganizing. Shibata agrees with Frank and Magnus that the fungus is digested by the host, in a manner analogous to the digestion of insects by carnivorous plants. He regards amitosis as another type of cell activity, not necessarily pathological. Hiltner's results agree with the above. He thinks that only certain portions of the fungus — Janse's sporangioles — are digested by the host. He regards nitrogen enrichment as proven in the case of Podocarpus.

NEGER[33] combats the well-known view of Stahl that there is a struggle for food salts in the soil between root hairs and fungi, in which the latter are most successful. Stahl supported his contention by showing that autotrophic plants grow better in sterilized soil than in soil permeated by fungi. Neger claims that this is due to the greater abundance of foodstuffs in sterilized soil. *Lepidium sativum* and *Triticum vulgare* were grown in (*a*) non-sterilized forest mold, in (*b*) similar but sterilized soil, and in (*c*) a mixture of *a* and *b*. The plants grown in *a* were far less luxuriant than in *b* or in *c*, though the roots were equally developed in all cultures. The equal development of cultures *b* and *c* shows that the presence of fungi scarcely restricts the activity of root hairs, as Stahl supposed. — H. C. COWLES.

[30] SHIBATA, K., Cytologische Studien über die endotrophen Mykorhizen. Jahrb. Wiss. Bot. **37**: 643–684. 1902.

[31] HILTNER, A., Beiträge zur Mycorhizafrage. Naturw. Zeits. Land- und Forstwirthschaft **1**: 1903 (Bot. Centralbl. **92**: 250).

[32] See BOT. GAZ. **32**: 377. 1901.

[33] NEGER, F. W., Ein Beitrag zur Mycorhizafrage: Der Kampf um die Nährsalze. Naturw. Zeits. Land- und Forstwirthschaft **1**: 372 ff. 1903 (Bot. Centralbl. **93**: 542).

NEWS.

PROFESSOR JOHN M. COULTER, after an absence of nine months, most of which was spent in Europe, has returned to his duties at the University of Chicago.

CHARLES L. POLLARD has left the U. S. National Museum to become a member of the scientific staff of the G. & C. Merriam Company, a publishing house of Springfield, Mass. His relation to *The Plant World* remains unchanged.

NATURE for November 5 gives an account of the eighty-sixth meeting of the Swiss Association for the Natural Sciences at Locarno. Mr. E. Fischer of Berne read an interesting paper on the origin of species, especially as illustrated by the Uredineae.

WITH REGRET we announce that the December number of the *Journal of Applied Microscopy and Laboratory Methods*, established by the Bausch & Lomb Optical Co. in January 1898, will terminate its existence. The *Journal* has been of much service to biologists in disseminating information as to methods and equipment of laboratories.

AMONG THE papers of botanical interest at the Cassel meeting of the German Association for the Advancement of Science and Medicine may be mentioned Professor Drude's account of his experiments on mutation, in which he gives results differing from those of DeVries. He thinks there is no sharp line between variation and mutation.

WITH ITS SECOND VOLUME the *Forest Quarterly* becomes an independent journal, being published privately under the direction of a board of editors, with Professor Fernow as editor-in-chief. The board well represents the profession of forestry and includes men from the various centers of professional forestry work. The journal deserves the support of all those interested in this great and growing subject.

DR. J. N. ROSE, of the National Museum, returned last fall from his fourth journey to Mexico, having made an unusually large collection of plants, comprising over 1500 distinct numbers. He also sent to Washington more than 200 living plants, mostly Crassulaceae, probably representing the richest collection of such plants ever sent from Mexico. The type locality of nearly every species of north Mexico was visited, and living material was obtained from most of them.

THE new way of extracting turpentine, introduced two years ago by Dr. Charles H. Herty, working under the direction of the Bureau of Forestry, is resulting in a complete change of methods by turpentine operators all over

the south. The economic saving of this new method is enormous. Not only is there a great increase in the amount of turpentine produced, but it is an important factor in saving the pine forests of the south. Trees from which turpentine has been extracted by the old method soon die from the wounds inflicted on them. The new system, on the other hand, is not fatal to the tree, and does very little damage to the timber.

THE LAST ISSUE of *Science* for 1903 publishes the list of grants made by the Carnegie Institution. Those for botany are as follows: W. A. CANNON, New York Botanical Garden, for investigation of plant hybrids, $500.—H. S. CONARD, University of Pennsylvania, for study of types of water-lilies in European herbaria, $300.—DESERT BOTANICAL LABORATORY (F. V. Coville and D. T. MacDougal, directors), $8,000.—E. W. OLIVE, Crawfordsville, Ind., researches on the cytological relations of the Amoebae, Acrasieae, and Myxomycetes, $1,000.—JANET PERKINS, working at the Royal Botanical Gardens, Berlin, for preliminary studies on the Philippine flora, $1900.—G. R. WIELAND, Yale University, for continuation of his researches on living and fossil cycads, $1,500.

TESTS to determine the strength of the principal American timbers used for construction purposes are now in progress at Washington, at Yale University, at Purdue University, and at the University of California. The Bureau of Forestry, under whose direction these tests are made, plans to make tables of the strength of different American woods in cross bending and breaking, compression with and against the grain, and shearing. No complete and satisfactory series of tests on large sticks of timber has ever been made in this country. Lumber manufacturers in the south and the Pacific coast states are especially interested in this work, and have contributed gratis much of the material. The chief timbers now being tested are the southern pines and the red fir of the Pacific coast. In the laboratories at Washington tests are now in progress on loblolly pine sticks 17 feet long and 8 by 14, 8 by 8, and 8 by 4 inches. Special attention is given to the effects of moisture on the strength of wood. The timbers tested are of the usual grades offered in the market and are not selected pieces. At the laboratory of the Yale Forest School small selected pieces of longleaf pine, without knots or other defects, are being tested as to the ultimate strength of the fibers. At Purdue University tests are being made with hardwood timbers.

IN THE early morning of December 11, Marsh Hall, occupied by the Yale Forest School, was seriously damaged by fire, which started in the basement and involved the entire four stories of the building. The damage was chiefly to the furnishings and the interior finishing of the building, though the various collections and the laboratory equipment of the Forest School also suffered. Fortunately the library, the equipment of the botanical laboratory, and the herbarium were but slightly damaged. A large collection of South American woods and a collection of west American conifers, all of which were in large

blocks, were destroyed. The specimens of domestic woods were discolored by smoke but not otherwise injured. Many tools and much apparatus, the greater part of which can be replaced on short notice, were totally destroyed. The technological laboratory was badly injured, but much of the machinery can be repaired. One of the heaviest losses was the complete data, covering six months' work by an expert and two assistants in the technological laboratory, where in cooperation with the Bureau of Forestry a study is being made on moisture and volatile oil in relation to the strength of timber. A large force of men is already at work in repairing the interior of the building and all classes will be resumed without interruption at the opening of the term on January 9.

THE NEW YORK BOTANICAL GARDEN has secured a lease of the group of buildings at the Cinchona Botanical Garden belonging to the Colonial Government of Jamaica and will maintain them as a botanical laboratory under an agreement with the Colonial Government, and with the cooperation of the Department of Public Gardens and Plantations of Jamaica. Sufficient land for experimental purposes and for a nursery is included in the leasehold privileges. The buildings include a residence known as Bellevue House, three laboratories, two ranges of glass, and small buildings suitable for lodging. Investigators are there offered the use of tables in the laboratory buildings; lodging in Bellevue House or in one of the other buildings at Cinchona; the use of land for experimental purposes; privileges to study the plantations at Cinchona, and also those at Hope and Castleton Gardens; privilege to consult the botanical library of the Department of Public Gardens and Plantations at Hope Gardens, and to take books therefrom to Cinchona under such conditions as may be imposed by the Director of Public Gardens and Plantations; easy access to an immense number of indigenous species in the primitive forests adjacent to Cinchona.

All persons who may apply for permission to study at Cinchona must submit such evidence as the Director-in-Chief of the New York Botanical Garden may require that they are competent to pursue investigations to advantage. While in residence at Cinchona they will be under the supervision of the Hon. William Fawcett, Director of Public Gardens and Plantations, to whose interest and advice the establishment of this American tropical laboratory is largely due. A laboratory fee, payable to the New York Botanical Garden, will be required of persons granted the above privileges.

Upon approval by the Scientific Directors of the New York Botanical Garden, any other institution, society, or individual, may be assigned the use of a table at Cinchona by the payment of $100 annually, which will entitle them to nominate investigators without the payment of fees; but not more than one person may be granted the use of any such table at the same time. The necessary expenses for a month's residence at Cinchona, including traveling expenses to and from ports on the Atlantic seaboard of the United States, are from $140 to $200; for two months' residence $160 to $230.

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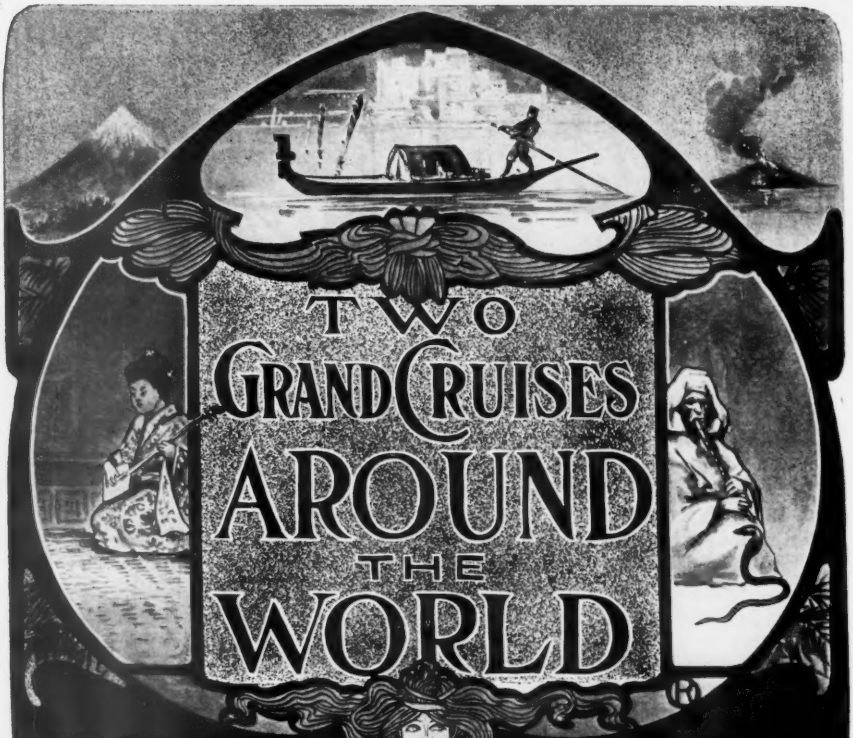

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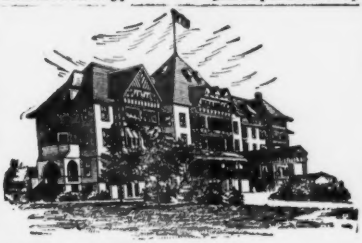

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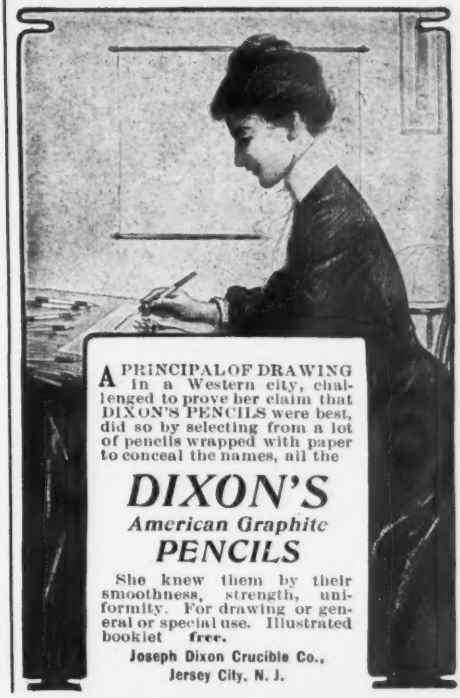

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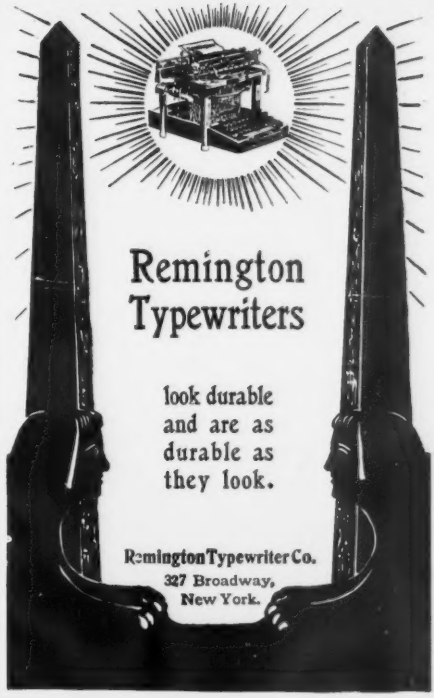

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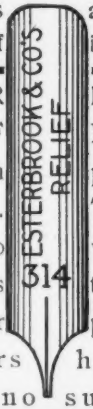

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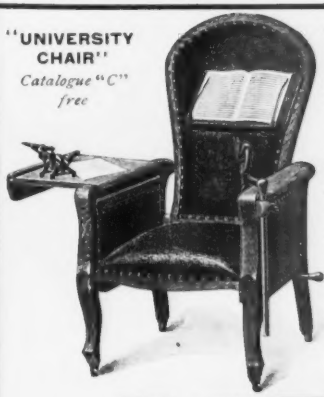

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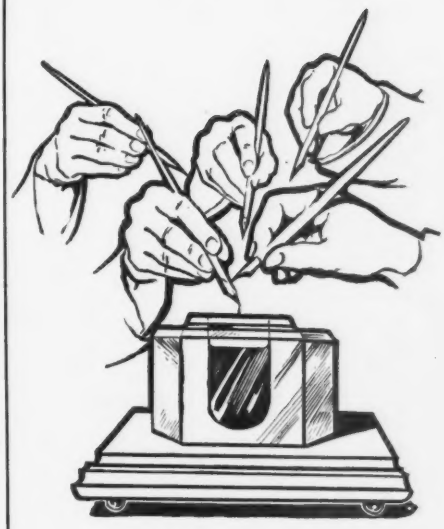

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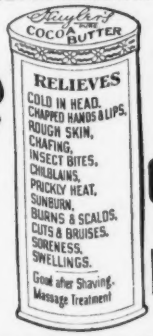

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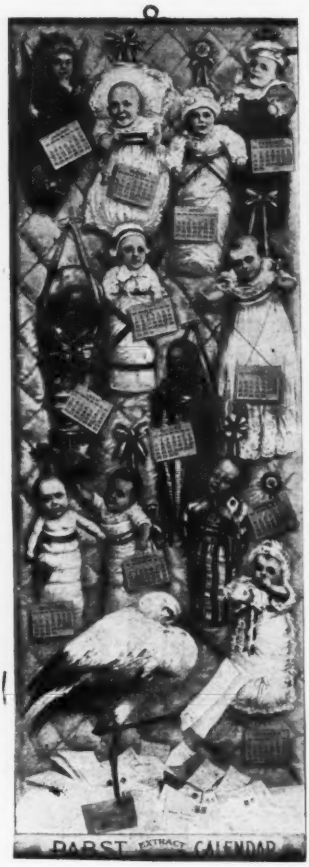

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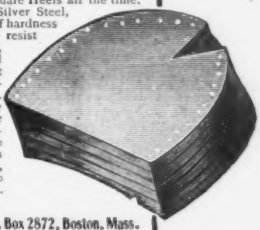

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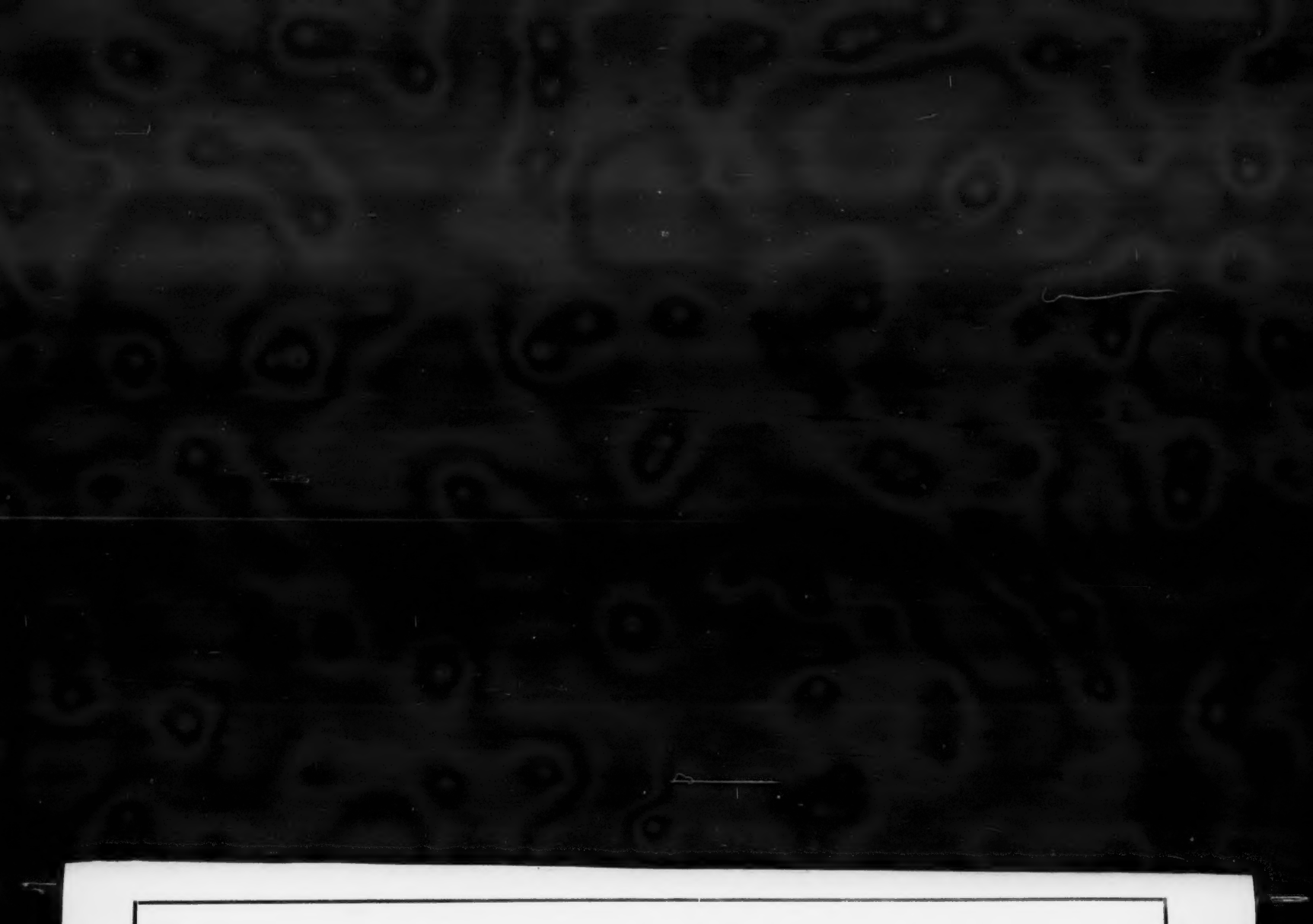

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